

Fauna and Flora of the Bay of Naples

Cephalopoda

Embryology

Part I, Vol. II

[Final part of Monograph No. 35]

ADOLF NAEF

1928

ZOOLOGISCHE STATION ZU NAEPEL
Zoological Station, Naples

FAUNA AND FLORA OF THE BAY OF NAPLES

[Fauna und Flora des Golfes von Naepe]

Monograph No. 35

CEPHALOPODA

EMBRYOLOGY

Part I, Vol II

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by
ADOLF NAEF
1928

(Systematic morphology of the external organization and of the mantle cavity, including consideration of the shell and its relationship with the soft body. Special descriptions of the *embryonic* forms, with particular regard to molluscan phylogeny and general principles of comparative ontogenetic studies)

WITH 142 TEXT FIGURES AND 37 PLATES (THE LATTER ORIGINALLY
PUBLISHED IN 1921 IN VOLUME ONE)

Translated from German



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DIE CEPHALOPODEN

VON
ADOLF NAEF



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BERLIN

1928



Foreword to the English Edition

Clyde F.E. Roper

The publication of this volume represents two significant events. First, it is the completion of the translation of the monumental monograph by Adolf Naef, the Swiss zoologist who, above all others, shaped the very foundation upon which modern cephalopod systematics, classification, evolution, morphology and embryology are grounded. Second, it represents the culmination of the series of translations into English of monographic works on Cephalopoda, begun in 1972 with the publication of the first volume of Naef's monograph, *Systematics*, in two parts (1921, 1923). It seems entirely fitting that the series of translations be completed with Naef's *Embryology*, Volume 2 (1928).

The Smithsonian Institution Libraries sponsored the translations of eight major monographs on cephalopod systematics, for which service I express my gratitude and appreciation. These translations have brought among the most important, seminal 20th Century works on cephalopods into the hands of researchers and students around the world. They comprise the following: Naef, A. 1921/1923 (1972), Chun, C. 1910/1914 (1975), Pfeffer, G. 1912 (1993), Joubin, L. 1895, 1900, 1920, 1924 (1995), and Naef, A. 1928 (2001).

The Translator and Scientific Editor for this volume is Sigurd v. Boletzky, to whom I am most deeply indebted and most sincerely appreciative for the thorough, accurate and very significant effort he put forth to insure that this translation accurately reflects Naef's meaning and intentions. Those who have tried to read Naef in the original German will especially appreciate the results of Boletzky's efforts. Early 20th Century German language, especially scientific, is very complex, convoluted, even archaic. Sentence structure tends to be long, nearly paragraphic in style. Boletzky has done a magnificent job in converting this to modern English, both in meaning and structure. Even so, an accurate translation, faithful to the scientific and philosophical

intent of the author, means that the reader occasionally will be challenged. Some sentences remain long, convoluted, Germanic, because, without apology, it has not been possible to reconstruct them without altering the meaning. Finally, Naef placed great reliance on remarkably accurate and detailed illustrations produced from living and preserved specimens, and these must be referred to continuously in order to fully understand the text.

Boletzky has provided a biographical sketch of Adolf Naef in this volume. This well-researched piece gives a sense of both the breadth and depth of Naef's knowledge that spanned invertebrates, vertebrates and fossils. It reveals Naef as one of the most accomplished zoologist of his time, whose career and productivity were cut short by politics and war.

April 2000

National Museum of Natural History
Smithsonian Institution
Washington, D.C.



ADOLF NAEFF

(1910; from the Archives of the Naples Zoological Station)

Adolf Naef (1883–1949)

A Biographical Note

S.v. Boletzky

Many German-speaking zoologists remember the work of Adolf Naef, especially if they are interested in morphological studies relating to molluscs or vertebrates. The cephalopod monograph in the series "Fauna und Flora des Golfes von Neapel" is a widely recognized work of reference. Much of Naef's later work on the morphology and phylogeny of vertebrates has been used in modern textbooks and reviews.

Naef was an eminent scientist, so it is not surprising to find his name in the German encyclopaedia "Der Grosse Brockhaus" (Vol. 13, page 144, 1932): "Naef, Adolf, zoologist, *Herisau (Switzerland) 1st of May, 1883; 1922-26 ass. Prof. in Agram, since 1927 Prof. in Cairo. N. strives to revise the assumptions and principles of morphology and phylogeny, using especially the examples of cephalopods and vertebrates. His most important publications are: "Idealistic Morphology and Phylogenetics" (1919), "The Fossil Cephalopods" (1922), "The Cephalopods" (35th monogr. in 'Fauna and Flora of the Bay of Naples', Vol. 1, 2, 1921-28), "Phylogeny of Animals" ('Handbook of Genetics', Vol. 3, 1931)".

Some personal data are provided by an entry in "World Biography" (1948): "Naef, Adolf, Swiss zoologist, born May 1, 1883, Herisau, Switzerland; son of Martin & Berta (Rutz) Naef; educated at Institut Steinegg, Herisau, 1900; Evangelical Seminary, Zurich, 1903; University of Zurich, 1908; married Maria Bendiner, July 22, 1924; two daughters. Research worker, Zoological Station, Naples, 1910; Privatdozent, University of Zurich, 1914; Prosector & assist. Prof., University of Zagreb, 1922; Prof. of Zoology, Univ. of Cairo, 1927; visiting professor of Comparative Anatomy and Embryology, Faculty of Science, University of Cairo, since 1940. Director,

Zoological Dept., University of Cairo, 1929-40. Member Swiss Association of Zoology; Swiss Association of Natural Science; Cairo Scientific Society”.

The apparent “early retirement”, at age 57, reflects the governmental regulation due to which foreign professors at the University of Cairo lost their positions soon after the beginning of World War II. They were given the status of “visiting professors” and were allowed to continue their research—as far as that was possible in the war-time—and to supervise their post-graduate students, but it was virtually out of the question for them to travel. After an almost total scientific isolation throughout the years 1940-45, Naef was finally able to resume his international contacts, travel to Europe, prepare the publication of his long-planned Textbook of Vertebrate Zoology, which was already cited in the reference list for “World Biography”. But then his health failed. Dangerously ill he returned to Zurich in spring 1949; he died on May 15.

What the biographical notes available do not mention is a major disappointment in Naef’s career as a university professor. In 1930, he was not only “short-listed” for the chair of zoology at the University of Basle (Switzerland) — he was in fact number one on the list! However, local events allowed that order to be turned over in favor of a younger candidate. Undoubtedly Naef’s scientific impact would have been different in subsequent decades if he had been allowed to continue research and teaching in a European university. A fair confirmation rests in the fact that his published work has not aged.

It is significant that Naef is regularly cited in modern studies, for example in the Centennial Essay by K. Nübler-Jung and D. Arendt, titled “Is ventral in insects dorsal in vertebrates?—A history of embryological arguments favoring axis inversion in chordate ancestors” (Roux’s *Arch. Dev. Biol.*, 203: 357–366, 1994): “During the first decades of the twentieth century, phylogenetic speculations based on embryogenesis were generally despised. Nonetheless, some 50 years after Anton Dohrn, the Swiss zoologist Adolf Naef (1883–1949) endeavored to revive Dohrn’s “annelid hypothesis” of chordate ancestry — which he considered a truism beyond discussion. Naef aspired to work out the “archetypal” ontogenesis of an “idealized” primeval coelomate of bilateral and segmented organization, suitable as a common ancestor of both annelids and chordates (Fig. 7: “from Naef, 1926”). From this archetypal ontogenesis he then derived the mode of embryogenesis in an idealized ancestral chordate (Fig. 8: “as above”). As for the bodily “revolution” during chordate evolution, Naef proposed that the worm-like chordate ancestor lived buried in sand or mud where constant dorsoventral orientation was of no importance, as is the case in some living hemichordata, e.g. *Balanoglossus* (Naef, 1933).—Note that the terms “archetypal” and “idealized” do not mean that Naef returned to the principles of the idealistic morphology as claimed by

Mayr (1982). Rather, Naef's aim (like that of Dohrn) was to reconstruct, on the basis of comparative embryology, the specific course of possible ontogenetic changes in the evolution of chordates from an annelid-like ancestor...".

In "The Growth of Biological Thought" (1982), Ernst Mayr had indeed expressed the following opinion: "...authors like Naef, Kälín, Lubosch, and Zangerl virtually returned to the principles of idealistic morphology", and reflecting on morphology in general, he wrote: "Nothing illuminates the difficulties of assigning morphology to a particular area of biology better than the lack of communication among different of its schools. There were the phylogenetic morphologists, like Gegenbaur, Haeckel, and Huxley (up to Remane and Romer); there was a strong remnant of idealistic morphology (Naef, Kälín, Lubosch), and there were the evolutionary morphologists (Böker, D. Davis, Bock, von Wahlert)...". Authoritative "classifications" like the one cited here may have been fashionable for some time, but they are certainly rather questionable. As far as Naef is concerned, his careful reassessment of "idealistic morphology" should not be taken as the sole content of his method!

In a recent review (Aufs. u. Red. Senck. Ges., 1998), W.-E. Reif scrutinized the question of Naef's alleged return to pre-Darwinian morphology: "In the German literature (between 1910 and 1960) macroevolutionary theories were proposed that regarded "types" as autonomous entities of evolution. Selection and adaptation played only a minor role, but orthogenesis, life cycles of types, revolutionary jumps from type to type and long-lasting Lamarckian effects were regarded as main factors of evolution. Usually these macroevolutionary theories were justified by reference to Adolf Naef's "Idealistic Morphology" and his concept of the type. However, a close look at Naef's methodology shows that it forms the basis of a Darwinian, structuralist morphology, rather than a mystical, speculative "typology"."

Among the motives for the remarkable scientific growth of Adolf Naef, probably his genuinely critical mind was foremost, but the intellectual environment in which he lived also was crucial. As a student, Naef "learned" his zoology in a very stimulating atmosphere at the University of Zurich. His university teacher was Arnold Lang, a former Professor of the Jena University and close friend of Ernst Haeckel, but definitely not a "fervent disciple". In his young years, Lang had been an assistant of Anton Dohrn, the founder and first director of the Zoological Station at Naples. This personal relationship was instrumental in the establishment of regular collaboration between the institutes at Zurich and Naples. In 1908, Naef went to Naples for the first time, originally to collect eggs of various marine molluscs to complete his Master's thesis. But he became rapidly involved in an embryological study on the squid *Loligo vulgaris* and finished his doctoral dissertation on that subject in about one year! He was then offered the position of a permanent visiting scientist at the Naples Station to com-

plete a cephalopod monograph that had remained unfinished after the untimely death of Giuseppe Jatta. Naef accepted this offer, but he soon realized that his scientific background was too different from Jatta's to allow him a mere completion of a work not designed by himself. His decision to start a new monograph was accepted by the director of the Naples Station, but it meant years of extra work, especially since Naef continued his general molluscan studies and actively prepared his enlisting as a university teacher at Zurich, with a necessarily regular publication activity. During the years of World War I, the working conditions at the Naples Station became so grim that Naef finally returned to Zurich, where Reinhard Dohrn, the exiled director of the Stazione Zoologica, had set up headquarters. After the war, Naef extended his morphological studies to fossil coleoids in the major museum collections, especially in Germany. As a result of this enterprise, he produced his paleozoological monograph of coleoid cephalopods.

By the time the first volume of the cephalopod monograph was published (1921, 1923), Naef had finished his "Studies on the general morphology of molluscs" (third part: 1924) and his book on fossil coleoids (1922). In 1922, he took a position at the University of Zagreb; henceforth his work dealt mainly with vertebrate morphology, generating a long series of detailed studies, reviews and methodological papers published from 1924 onwards. In 1926, Naef returned to Naples for a few months to write up the overdue monograph volume on the embryonic development of cephalopods (the embryology plates having been published already in 1921!). In the following years his interest in cephalopod morphology and phylogeny remained alive, but none of the further volumes he had announced would be produced. What Naef did achieve, however, was a first draft of a cephalopod chapter for Pierre-Paul Grassé's "Traité de Zoologie", which he wrote in the late forties.

That Naef kept abreast of ongoing cephalopod research can be seen, for example, from his correspondence with Grace E. Pickford (1902–1986) on the *Vampyromorpha*. A letter of January 1st, 1947, reflects his steadfast enthusiasm: "Dear Miss Pickford, With great pleasure I had received your publications on *Vampyroteuthis* and others. Although I am not now working in this field of research the subject is most interesting to me. I have not seen any specimen of *V.* myself and my statements on it were based entirely on other observers. Your figure of the gladius suggests that the animal belongs rather to the *Prototeuthoidea* than the *Mesoteuthoidea*. I am very thrilled to obtain a copy of your final account to which I am looking forward with great interest. I hope it will be well illustrated in order to give full evidence of the character of this unique animal.—With my best compliments—Yours sincerely—Prof. Dr. Ad. Naef". Some thirty years later, Grace Pickford concluded: "It is certainly time that recognition was given to this great man whose insight into cephalopod evolution was, to me,

almost a bible. Long before a translation was available I had a German-speaking friend who gave me verbal translations of those sections of his monograph that concerned the Proto- and Mesoteuthoidea. This information was invaluable to me in understanding the status of *Vampyroteuthis infernalis* upon which I was working at the time.—I was always glad that Naef lived to see that there was a living fossil that went far to vindicate his insight into cephalopod phylogeny”.

Fifty years after Naef’s death, a new generation of zoologists and paleontologists is eager to get to know his studies in detail. The present “Cephalopod Embryology” completes the English translation of the 35th monograph of the Naples series. Time to think of the cephalopod paleontologists who wish to read the “Fossil Coleoids”. An English translation of this classic will be made available through the book-trade.

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Translator's Notes

S.v. Boletzky

The technical terms used by Adolf Naef are easily translated (e.g. "Stadium" = stage, "Stufe" = grade) or may be adopted without any change (other than orthographic adjustments): e.g. "Anlage"=anlage (rudiment); "Bauplan"= bauplan (structural plan, blue-print); "Norm" = norm; "Ontogenese" = ontogenesis; "Phylogenese" = phylogenesis; "Reminiszenz" = reminiscence.

The nouns ontogenesis and phylogenesis are rarely used in English today, since ontogeny and phylogeny have become standing terms. Some dictionaries (e.g. 'Cassell's German & English Dictionary', 1964) still list ontogenesis (rather than ontogeny) for "Ontogenese". The commonly used translation phylogeny for "Phylogenese" also corresponds to "Stammesgeschichte" or "Phylogenie". 'Pennak's Collegiate Dictionary of Zoology' (1964) indicates two meanings for phylogeny: "1. Evolutionary relationships and lines of descent in any taxon. 2. The origin and evolution of higher taxonomic categories"; ontogeny is simply defined as "Developmental history of an organism from zygote to maturity". The last definition is compatible with Naef's terminology used in Volume I (p. 27): <<This "ontogeny", or individual "developmental history", is well known in a large number of cases>> (quoted from the English translation by A. Mercado, 1972). Accordingly, I have translated "Entwicklungsgeschichte" or "Ontogenie" as ontogeny, "Stammesgeschichte" or "Phylogenie" as phylogeny, "Ontogenese" as ontogenesis, "Phylogenese" as phylogenesis. A subtle difference of meaning between ontogeny and ontogenesis, or between phylogeny and phylogenesis, could be related to a distinction of pattern (ontogeny, phylogeny) and process (ontogenesis, phylogenesis).

The term "Urform" can be translated as archetype or prototype; archetypal is available as an adjective for the translation of "urbidlich" or "urtypisch". In Volume I

(p. 43) Naef stated: <<Indifferent (ambiguous) terms are also frequently used. An example is "prototype" (Urform), which can mean either "type" (ideal form, Typus) or "ancestral form" (Stammform)>> (quoted from the 1972 edition). This statement reveals a distinction which is implicit in the definitions given in 'Pennak's Collegiate Dictionary of Zoology': "archetype. Prototype"; "prototype. Primitive form regarded as ancestral to a particular taxon; archetype". Accordingly, "Urkonchifer" can be translated as protoconchifer, "Urcephalopode" as protocephalopod. Since Naef reasoned along the lines of modern phylogenetic systematics, one is often tempted to translate his "old-fashioned" terms into modern cladistic terminology. Of course, such an interpretative translation would be a false step (NB: Naef wrote his text a quarter century before Willi Hennig published his seminal book on the fundamentals of phylogenetic systematics, introducing a new terminology and recalling Naef's pioneering work to the reader).

To make Naef's bibliography easily exploitable, the titles of German, French or Italian papers and books have been translated. This source of information may be useful to anybody interested in the international nature of the scientific literature used by Naef, who had full command of all these languages (so he could have written the cephalopod monograph in English if that had been requested).

The outstanding quality of Naef's cephalopod embryology remains untouched by some flaws of the book, e.g. numerous misprints and some inconsistencies in numbers or titles of subdivisions, or in figure labels and legends. These defects are probably due to the material conditions under which the final version of this book went to the press (NB: Naef moved to Egypt in 1927, i.e. several months before the work was published). The translation tacitly passes over obvious typographical errors and misprints.

The pagination of the original text is given in the margin of the present translation, and all the page indications for other parts of the book refer to this original pagination (as for Volume 1).

Foreword

The present book is the second volume of my monograph of cephalopods and complements the first one, from which it had to be separated due to its length. Along with this separation, coherence of the work had to be maintained, however. Although the description of embryonic forms has not exactly the same practical and systematic significance as the previous description of postembryonic forms, which provided a general revision and reference volume allowing for species identification, early ontogenetic stages were in many cases of special interest for the recognition of the natural relationships, which are approached here from an explicitly historical point of view.

For a phylogenetically oriented morphology, early ontogenetic features are of truly fundamental importance, since there is a valid concept in the contention that ontogenesis represents an abbreviated recapitulation of phylogenesis. Elucidation of the problematic relationships expressed in this so-called "biogenetic law" was in fact the main target of the present study, beyond the factual coverage. These relationships not only were the guide through the maze of observed diversity, but they also were the object of a more general scientific interest.

This concern can be read between the lines throughout the whole work; it deserves particular attention in this introduction. Once the special coverage was achieved, it appeared necessary to consider again critically its theoretical background, and to present it in the most appropriate form (cf. Vol. 1, p. 3). This problem has been approached by the author in earlier publications, but a comprehensive review is possible only now based on the special investigations that helped to refine the concepts.

Probably no morphologist will doubt the need for a comparative description of cephalopod development. A detailed study of this subject has in fact never been published before, although many data are scattered in the literature along with some greater

special investigations. These are not intended to be dismissed by the publication of the present monograph, which is indeed not able to summarise the entire subject field. Description of the inner organisation—like anything else dealing with microscopic studies and analysis of histological sections—had to be postponed for the next volume of the monograph*. The present part thus presents literally superficial descriptions and covers the subject more in breadth than in depth; it could thus be disappointing for anyone expecting to find an answer to all the questions raised by modern embryology.

On the other hand, there was a wealth of new and interesting features to be observed in the surface structures of cephalopod embryos, and from the outset their careful study promised to yield insight into important facts and relations. If certain details are missing in this presentation, it certainly attempts to provide some compensation in the survey of a rather wide field. Combined with the previous volume, it should give an image of *unity* within the *diversity* of natural forms—something appearing so clearly in only a few groups.

This monograph thus attempts to gain in intellectual depth compared to pure accumulation of descriptions, by trying to grasp the diverse facts as a whole. This attempt has hopefully achieved something, so that further expectations can be reconciled with the prospect of future coverage in greater detail. For it is undeniable that descriptive zoology often cannot see the forest for the trees in pursuing extremely special questions. May the present attempt to survey the broad stream of living processes from a well-defined viewpoint, or to recognize the identities and relationships of a multitude of organic forms in their natural order, be judged on the seriousness of its aspiration and the coherence of the result rather than on the number of unfulfilled expectations!

This book considers its subject for its own sake and for the immediately resulting gain in knowledge. However, the detailed descriptions of surface features of embryos serve indirectly other aims as well: First of all, the description of organogenesis in Volume 3* thus will get its foundation, since the progressive development of organization will use the then-familiar total views and well-defined embryonic stages; thus only can inner processes be visualized in context. The reader indeed can not be expected to have all the special interest for the often very complicated and unusual topographical conditions in this animal group, without being assisted by these earlier figures when viewing the real objects in their natural appearance.

* Scientific Editor: Naef did not produce the third volume announced here (see biographical note).

Finally, the illustrated description of typical stages is also intended to lead the way towards *experimental* investigations into cephalopod development:

In addition to the special aims of systematic-morphological research, this volume indeed intends to serve a sister science, namely dynamic morphology, which generally is termed developmental mechanics. Occasional experiments performed by the author have shown that cephalopod eggs and embryos, when properly handled, provide an excellent material for a causal analysis of development.

Experiments similar to those successfully undertaken with amphibians by Roux, Harrison and Spemann and their students can be made on cephalopods, as will be discussed at the end of this volume. In this field, quite special questions arise for which special answers can be expected if the study is done by an experienced worker following an appropriate plan. One of the basic conditions for the achievement of such a research program is a detailed knowledge of the systematic morphology of the object; this condition was not always met in earlier work done on amphibian eggs, which considerably impaired some results. I believe that the present volume is an essential contribution to such preparatory work, and I hope to complete the missing details of inner organ differentiation in the near future, so that experimental investigations can be started in a well-prepared field.

The above remarks should not be taken to mean that this monographic study represents an entirely mature harvest. Numerous impediments have combined in reducing the results of this work. When I had to leave the splendid working conditions of the Naples Station in the ominous year 1916 that led to progressive dissolution of all human values, I was carrying an almost frightening wealth of manuscripts, notes, drawings, preparations and specimens, and I was filled up with knowledge that awaited its final shaping. I did hope to bring all this to a relatively safe island when I returned to my Swiss home country, and there to finish and publish the work to which I had devoted the best of my early years. Unfortunately, this proved impossible for many years during which I had to fritter away my time and energy in the dual struggle for a livelihood and for the achievement of a scientific task pressing heavily upon my limited resources.

Thanks to repeated financial support by the Naples Zoological Station, whose administration in its turn had to cope with very heavy oppression, and thanks to help — made possible again through recommendations by the Naples Station — offered by the Bavarian and Prussian Academies of Sciences, the Prussian Ministry of Culture,

and the Foundation for Scientific Research at the University of Zurich, and also with the help of my personal friends, it was finally possible to publish (1921 and 1923*) the first volume and the plates of the second—a fact for which I owe an immense debt of gratitude to all those who helped (cf. Vol. 1, p. xii). It was not possible, however, to publish the second volume immediately afterwards; this had to wait until the Naples Station had re-established the conditions necessary for the finishing and publication of this work, which was approaching its final stage already in 1917. A thorough revision of the manuscript was achieved in autumn 1926, and I gratefully acknowledge the support of all those who helped me through this revision and the preparation of the manuscript for the press. In particular I thank my wife for the laborious job of typing the definitive version, and I am also greatly indebted to my old friend Prof. Dr. J. Gross who undertook the final manuscript revision; thanks are also due to the printing firm Fr. Giannini & Figli in Naples and to their skilled workers. My entire scientific attitude benefited by the thorough influence experienced during my last Naples sojourn from the close contact with the Privy Councillor Prof. Dr. K. Heider, with whom I was allowed to share an idyllic duplex household. I shall never forget the friendly and ingenious atmosphere that I enjoyed there. Special thanks finally to the Naples Station, and in particular to the Director Prof. D.R. Dohrn for his kind support throughout my work.

Due mainly to the special facilities offered by the Zoological Station, a fairly rich and fine material can be described here. This is true for the embryonic development of *Loligo vulgaris*, which is the most easily available form (Plates 1–7) but whose outer embryonic features have never been described in comparable detail, since most embryologists underestimate the significance to their science of a thorough study of surface structures of the embryo. Entirely new is the description of the embryos of two oegopsid squids, one of which (Plate 8) has not been identified (cf. Vol. 1, p. 161), whereas the second (Plates 9–12) is an ommastrephid squid, probably *Ommatostrephes sagittatus***.

The development of the germinal disc in the common cuttlefish *Sepia officinalis* (Plates 13–22) also offered a number of new aspects, which may surprise us given the

* Scientific Editor: The first fascicle (1921) contained the introductory sections and pages 1–148 of the first volume along with the plates of the first and second volumes. The second fascicle (1923) was the rest of the first volume. Later binding has re- or disassembled these parts in some library copies. For citation, “Part I, Volume 1: Systematics” of the monograph can thus be dated either “1921/1923” or “1923” (meaning the complete volume).

** Scientific Editor: Now *Todarodes sagittatus*.

general familiarity with this material. But special concentration on the study* of surface structures allowed me to distinguish details that would go unnoticed by a less biased observer.

The description of *Sepiola* embryos (Plate 23) is again entirely new. It would have been easy to further complete this presentation, but the limitations of time and conditions permitted only selected descriptions and figures providing some comparative aspects to be seen in parallel with *Sepia* and *Loligo*. In contrast, it was possible to provide a completely new, detailed illustration of *Octopus* development (Plates 24–30), and to give figures of selected *Tremoctopus* and *Ocythoë* stages (Plates 31 and 37). The closing part is a very detailed description, which was so far lacking, of the development of *Argonauta argo* (Plates 32–37), providing the basis for comparisons with the development of *Octopus* and of different decapods; this should permit definitive elucidation of the problem of the origin of this peculiar cephalopod, at least to those morphologists who do not feel obliged to defend some preconceived ideas.

In conclusion, this volume is sent out to the world hoping that it will prove a useful element in the edifice of Science, thus justifying the considerable sacrifices that have been made for its achievement.

Naples,
July 1928

Adolf Naef

*Scientific Editor: The original text reads 'Stadium' (=stage) but probably means "Studium" (=study).

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* More detailed disposition at beginning of greater chapters.

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5.	<i>Sepiola</i> and <i>Sepietta</i> (Pl. 23)	432
6.	<i>Octopus vulgaris</i> (Pl. 24-30)	434-447
7.	<i>Tremoctopus violaceus</i> (Pl. 31)	448
8.	<i>Argonauta argo</i> (Pl. 32-36)	450-459
9.	<i>Argonauta</i> and <i>Ocythoë tuberculata</i> (Pl. 37)	460

** At the end we add the title page and general figure legends of the atlas, since they were not clearly identified as belonging to the second volume when they appeared with the first fascicle (1921), in which the plates were published. During binding these pages were often misplaced, be it in the first or in the united first and second parts of volume 1 (1923).

1

I. INTRODUCTION

3 1. General Aspects and Basic Concepts

Although this volume of the cephalopod monograph is mainly devoted to special descriptions of external embryonic body forms, it is also concerned—like the first volume—with a more general theme (see Vol. 1, p. 1). While the whole monograph is an attempt to gain new *foundations* for the *elaboration* and *assessment* of *phylogenetic theory* through broadly based systematic studies, this part deals more particularly with the aspects and results of comparative embryology, i.e. with the methodology and theory of a domain that is imposing as part of the greater whole; likewise the subject of this volume represents a section of the entirety of phenomena to be dealt with.

On closer scrutiny the relationship of this domain with others appears not so clear and straightforward: outer influences rather than the logical structure of investigation have historically placed *embryology*, as an independent field of research and teaching, opposite to *systematics*, comparative *anatomy* and *paleomorphology*, and merely practical considerations continue to cause a certain separation. One has to realize that the latter is not based on any principle that could justify separate consideration of the relevant problems from several *points of view* (with the idea that congruence of statements made on such different grounds would *therefore* give them greater weight for reasons of pure logic).

The way of thinking that underlies *systematic embryology* is the same as in systematic (comparative) morphology (indeed systematic biology) in general, but applied to a special group of phenomena.—Objectively a clear-cut separation of embryology is impossible and useless: A comparative anatomy that would neglect individual ontogenesis could have no place in a science of order dealing with the totality of life forms; over and over again it would inevitably be pushed across its artificial border lines. These are inconceivable for any comprehensive consideration—this is a crucial

point we have to make here. We *must* accept the naturally given facts. We encounter them as rigid *post mortem* forms, whereas living beings are undergoing continuous change (development).

Development is the cumulative, slow modification of the living form caused by irreversible processes; this form is *built* by means of growth, division and differentiation, and by the secretion of non-living, relatively firm parts; it is *dismantled* by degeneration, fusion, compensation, partial necrosis or rejection and resorption.

Form is the positional relationship among parts of the body, so far as it is maintained between such parts in the living organism even through temporary (physiological) modifications.—Thus morphology does not deal with a special kind of organizational geometry independent of the material features of components, or of their consistence and color; morphology deals with form as something analogous to the (effective) *construction* in mechanical engineering.

Description of forms implies dismemberment; the spatial correlation of parts thus revealed is termed 'bauplan'. The **bauplan** is the positional relationship among the major parts of the body in a normal, viable organism or in its parts, representable by a more or less rough (schematic) diagram.—Of course the difference between coarser or finer components remains undefined here. All gradations are conceivable and indeed necessary, as will be seen later.

These are basic concepts of the description of form in general.

Comparative morphology thus always has to integrate development, no matter whether the particular aim is formulation of the natural system, or description of typical adult stages within groups, or search for relationships between developmental stages or their relation with 'finished' animal forms. *Comparative morphology can only be the comparative study of development*: the actual objects of morphology are always developmental stages, and the study of rigid forms, i.e. cadavers (or fossils) is only an auxiliary means.

To be able to recognize and describe development, it has to be divided into "stages". This is a concession made to the limits of human imagination. For in nature there are, strictly speaking, no separate states; there are processes, but in general their features are so complicated that we can grasp and describe them only by means of such a dissection. Another way of viewing development could be the consideration of
5 (labile) balance conditions of living beings over given, rather short, periods of time;

thus even in morphology a more static representation of form creation could be confronted with a more genetic representation—However, a thorough analysis of the phenomena is achieved only if we consider all stages as parts integrated in the whole process of life history.

There is a justifiable tendency to consider form creation as something basically different from other organic processes, so that development appears as something *passively* ‘happening’ when compared to the ‘action’ of a fully developed apparatus. An ultimate synthetic view of vital phenomena will nevertheless have to restrict such a representation, although the difference between self-construction and other types of work is undeniable and indeed permits to oppose the mechanisms of development to those of operation (physiology).

The organism must of course be viewed as a living being during all the phases of its existence, structure and performance being linked up closely and inseparably. Clearly, the former determines the latter: either completely and unequivocally, if life follows exclusively mechanical and chemical-physical laws, or only partly, but still essentially, if additional, harmonizing factors are involved to generate order. At any rate, the linkage of apparatus and performance is continuous, hence the *continuity* of form is complete; there is no unstructured, homogeneous ‘living matter’ or ‘substance’; there are only living compounds of defined structure and function, the latter being explainable—if at all—only via the former.

It is true that any form is itself the product of some performance, but only as the product of work achieved by some pre-existing form. Therefore morphological consideration has absolute primacy over physiological consideration. *Form necessarily results from form*, but from the particular features of one form do others result partly or entirely. This is the basic law of matter, and above all that of living matter and its processes which appear as continuing formation (as ‘development’). It is really too simple to invoke physiological theory each time we can’t see any structure. That energy is converted is self-evident, but this conversion alone cannot define the peculiarity of life! Here indeed no other energies than those known from the inorganic world are observed or can profitably be presumed to exist!

The most general type of form change seems to be the *cyclic development* of the cell, which periodically—through great or small, simple or complex periods—adopts again and again states that are identical in form and potency to previous states, or at least resemble them to an extremely high degree. Therefore one can also call it a

rhythmic development, and this indeed appears as an essential condition for the continuity of life; but this does not of course solve the very problem of continuity, i.e. the logically inherent, inevitable question about the particular nature of this *persistence* that underlies the endless recurrence of the same.

The rhythmic-cyclic prototype of genesis (its complication by sexual phenomena can be neglected here) is periodically followed by a *terminal* development or 'ontogenesis', especially in multicellular forms; thus the rhythm of genesis undergoes an apparently secondary but immensely diverse enrichment. The latter again generates variable forms continually, but these forms rise from an 'anlage' to a climax state to finally approach decay, which offers special possibilities.

This terminal development is aimed at the establishment of auxiliary means or *apparatuses* for the *intensification* and *protection* of the life process. Since these blind-ended side-tracks no longer return to the continuity of the general path, they are free to evolve and to attain (through *division of labor*) a degree of technical specialisation impossible in uninterrupted cell cycling, which is not allowed, as it were, to depart too much from its perennial basis.—(On the relation between cyclic and terminal development within complete sequences of generations, see also Vol. 1, pp. 27-29!).

Here we disregard the fact that even within cell cycles terminal processes do occur, by which cell organs are driven to a high differentiation to be finally destroyed. In this process, especially in highly organized, multinuclear protozoans, we often observe regularities similar to those known from the terminal development of Metazoa and Metaphyta (cf. 1913, pp. 366-367; 1917, p. 63!). Beautiful examples are given in the monograph of the Acantharia by W. Schewiakoff, Naples, 1926.

The diversity of terminal (ontogenetic) formation is immense compared to the (at least seemingly) simple structures of cyclic cell development, and even an individual ontogenesis often exhibits a complexity of states and modifications that is difficult to grasp; hence the search for the natural organization of the observed facts.

Description of the individual, factual ontogenesis is merely prepared by its subdivision into stages, which represent cross sections cut on its course; additional auxiliary concepts of division and are indeed necessary. The great difference between the phases of development is expressed in the appearance of a distinct bauplan for each phase, so that we can follow the modification of bauplans in more or less finely graded steps and comprehend it in context. In analogy to the linkage of simultaneous parts
7 of the bauplan, we project the sequential appearance of parts into the '*ontogenetic*

plan', which is thus defined as the given sequence of bauplans characterizing the natural development of a living being. Ontogenesis is thereby viewed as segmented along with being viewed as integral, its representation thus preparing ground for detailed comparison and causal analysis.

In the orderly whole of bauplans and ontogenetic plans, parts and stages have their well-defined position. This position has to be considered in a particular way when different living beings are compared. For neither the relation of wholes nor that of parts must be disregarded, and therefore auxiliary concepts are necessary for such *comparisons*. These auxiliary concepts are of special interest when comprehensive, striking or peculiar, problematic similarities are under consideration; their *methodological conditions* become particularly clear wherever these similarities are rather complete. In such instances we easily state a *congruence of bauplans* of certain developmental phases, e.g. of the "finished organism", and a *congruence of ontogenetic plans* in the course of development in general. Indeed organisms are not subdivided into some very similar and some very dissimilar parts; but if an essential part of the construction clearly reflects the same plan, then the whole does so too.

Similarity of plan is based on a given formal (existing in idea) relationship of the parts, from which it is inseparable, this we term **homology**:

If two organisms are constructed according to the same plan, we consider a given part of the one homologous to a given part of the other, provided that both parts are represented by one in the common plan.

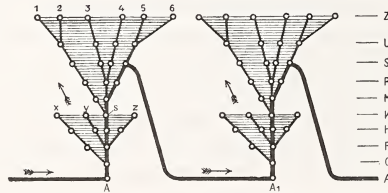
The homology concept has been misused extremely often, or has been placed in wrong context by confusing considerations (see 1926, *Biol. Zentralbl.*, 46: 405 follow).

Its special application is particularly significant to us in comparative ontogenetics. Its logical nature permits this application without doubt, since we recognize that ontogeneses can be viewed as segmented wholes, whose parts are the individual stages*, their unification being expressed in the ontogenetic plans: like homologous organs having congruent positions to one another and to the whole of a simple bauplan, similar stages are integrated in a congruent manner into the common ontogenetic plan. This leads to the concept of **homologous stages**:

* Scientific Editor: Here Naef introduces a new image of 'stage', calling it a 'segment', which is different from the earlier suggested 'cross section'; only the latter corresponds to our current use of the term *stage* in a developmental context (In etymological terms, however, 'segment' would be the correct translation of 'stadium', which is the latinized Greek 'stadion', meaning a unit distance).

If two organisms develop according to the same plan, we consider a given stage of one as homologous to a given stage of the other, provided that both stages are represented by one in the common ontogenetic plan.

This extension of the homology concept is, after all, binding for any morphology: only homologous stages permit, strictly speaking, discussion about homologous parts, and *vice versa*; this leads to the obligation to follow these homologous parts themselves through ontogeneses and to consider the latter as composed of parallel, partial processes or 'morphogeneses' (cf. 1913: 350–351); in the process of induction they form the actual material for the systematic consideration—material from which methodical comparison induces the natural order of relations.



Textfigure 1.—Schematic presentation of morphological relationships between two ontogeneses connected by the uninterrupted (cyclic) development of a "germ line" (From "Studien...", 1913, p. 351). The two trees* visualize the process of individual development of two metazoans, in which (starting from the fertilized ovum A, A₁) a series of larval formations (X, Y, Z) is produced; the anlage of the main mass of the prospective body (s) is not yet conspicuous; the definitive organs (1-6) arise only later.

Without the basal line (A-A₁), which continues forwards and backwards, the relational scheme is valid for two closely (formally) related ontogeneses in general. The line itself represents the observed or hypothetical continuity of germ line development, which proceeds rhythmically-cyclically partly across the metazoan body and partly outside it. This can best be compared to a root from which the individual ontogeneses periodically arise like sprouts. This representation is not supposed to stress an opposition between the germ and the soma cells, although it is very sharp in all higher animals. A germ line is present in any continuous cellular development, as compared to the formation of multicellular bodies derived from it. Thus the formation of homonomous elements, e.g. shoots (flowers) on the stem of a cormophyte, appears as a special case within the same context of fundamental relations. Using this scheme, one can finally compare the cyclic and terminal formations even within the context of cellular development; one will then have to deal with the question whether the ultimate cause of cyclic repeating is something plainly persistent, and what characteristics it might have (Cf. Naef, 1923, p. 396).

* Cf. diagram by Weismann (Naef, p.285) representing the cell genealogy in the ontogenesis of a metazoan to illustrate the "germ line". The present diagram is more generalised.

Morphogeneses are the developments of the individual body parts, so far as these parts can be considered distinct, either visually by direct observation, or by comparison

of similar species (showing these body parts as more or less independent form elements);
 9 *morphogeneses start out as visibleanlagen.*

Here one has to realize the true independence of individual morphogeneses whose stages can be shifted in relation to one another and then appear premature or delayed ('heterochronies'). This is true, to a rather limited extent, for the individual ontogeneses within one species; it is much more clearly true when different species, genera, etc. are compared. In general the extent of heterochronies increases with the distance separating the compared forms in the natural system.

Our special task here can only be to demonstrate the *regular relations* among a multitude of *ontogeneses*, which can then be comprehended in a *systematic context*. Extending the current concept, we basically apply the principles of natural systematics to ontogeneses (rather than to relatively rigid forms) and thus fulfill an essential requirement of the real objects (cf. above!). Since all living forms are variable, they have to be taken as such in a regular science conformable to nature, surely to provide correspondingly deeper insight under these conditions.

This basic consideration exists in its own right, independent of the experience that ontogenesis provides direct information about systematic relationships (e.g. according to the 'biogenetic law') or the opinion that the finished form can be explained based on knowledge about its development. Being is not explained by the mere reality of becoming, it can only be taken up by the latter. This consideration results from, as much as possible, the unbiased attempt to recognize the real objects as parts of the whole of nature. The first volume indeed showed that we have to engage in developmental systematics if we want to solve the practical problems posed by such a science. Even the diagnoses used in the natural system had to cope with *developing forms* (cf. Vol. 1, p. 260 and p. 725), so much the more the formulation of types (ibidem, pp. 232–236, 420–427).

The description of embryogeneses in the present volume shall therefore be, much like the representation of postembryonic forms in the first volume, a systematic description that proceeds deductively *from general to specific*. This builds on the system of the first volume which was often using rather more of the later developmental states; it should be emphasized, however, that the arrangement chosen there was already based essentially on the whole ontogenetic sequence. Its importance did not need to be deduced from a 'fundamental law'; it simply resulted from the general fact that the *preliminary stages* of structurally related forms are always much *more similar*

to one another than those resulting from them later on. They have a higher 'degree of generality' and thereby a particular systematic weight.

On the other hand, the general features of the early juvenile forms often entailed the practical *impossibility of precise identification*, so that for many of the youngest stages only the family could be recognized, for more advanced stages the genus, and only for the later stages was it possible to identify them to species. This had indeed to be taken into account in the arrangement of the identification tables (Vol. 1, pp. 812–821)! Ontogeneses placed in parallel can be arranged in a logical manner by using a system of more or less comprehensive diagnoses, i.e. definitions. This sometimes applies even to instances where such an orderly arrangement is not possible with the adult stages (cf. Vol. 1, p. 14).

After description of the bare facts, the inevitable first step to comprehension of greater connexions is the establishment of a system of subordinate and superordinate special concepts based on the congruences of bauplans existing between organic forms; this is achieved using the most straightforward and fundamental means of correct thinking, without hypothetical complication and confusion—Since we deliberately aim at a solid comprehension of phyletic relations, that is, a penetrating elucidation of the ontogenetic process and its regularities, we are in obligation to reject the amalgamation of systematics and phylogenetic speculation. Such speculation starts with muddling the very basis on which the sought-after understanding should develop (cf. e.g. Karny, 1925!).

As said before, systematic morphology does not limit itself to the systematics of species; it is the latter, however, that provides the most comprehensive relationships and gives promise above all to provide the ultimate synopsis of the ordinal coherence of the organic world.

The *systematic position of the individual species* is expressed by the series of its *systematic preliminary stages*, in fact by the immediately preceding one, which in turn is localized by the next preceding one, and so on. This relation has been emphasized elsewhere (1926, *Biologisches Zentralblatt*, Vol. 46: p. 205, p. 306) and does not need further discussion here (cf. Textfigure 3). Correspondingly the systematic position of two species in relation to one another can be comprehended by tracing them to the common preliminary stage, stepwise to be sure, which should never be neglected where comparisons are to be made methodically. This permits avoidance of vague statements about close or remote kinship, which made systematic (most often phylogenetically 'based') morphology into a playground of confused opinions.

In contrast to practical museum systematics, which deal at the most with bauplans but are not natural in the true sense of the word, our systematics must be based explicitly on congruence of ontogenetic plans. *Similarity of bauplan* means *congruence of several body parts or of whole organisms that are constructed according to the same bauplan*. In contrast, *similarity of ontogenetic plan* means *congruence of several body parts or of whole organisms developing according to the same ontogenetic plan* (at least during some early stages, whereas during later stages the original similarity of plans may decrease more or less drastically or even 'disappear' altogether). Degree of similarity of plans within natural groups is expressed by the respective abundance of diagnoses, which in turn corresponds to the approximation of the common plans to the complete picture of a real organism (p. 4).

In this respect, exclusive consideration of embryonic organizations indeed has its special advantages. Because development is virtually the sole performance of embryos, they represent the form purely as it were, untouched by the physiological complication that obscures the picture of further ontogenetic processes in "larvae" and in "finished" animals. Of course the separation of one phase from the other is not absolutely rigid, as will be seen in the special section; so much the more is it of interest to see which accompanying phenomena undergo some related variations.

On the other hand, morphological consideration of embryonic states presents special difficulties in the application of rigorous concepts such as those mentioned above. They are concerned in particular with the emergence of the anlagen in ontogenesis. We are accustomed to deduce each stage from preceding ones by observation of modifications in the respective positions of parts of the whole form; indeed the underlying 'mechanics' remain obscure in most cases, whereas the continuity of development opens a special way of understanding, namely the comprehension relating to association and incorporation of an aspect of form into the overall picture of nature.

The *plan-like regularity* of different ontogeneses in fact shows certain *discrepancies* in the first *emergence* of a differentiation that are not observed during the later course of development. In fact, we find that body regions with clearly defined homology are derived from parts of uncertain homology, or for which the assumption of homology must even be rejected; this represents a dangerous gap in our comparative method. Some renowned researchers have therefore called in question the entire way of thinking of systematic morphology, instead of carefully analyzing the problem or engaging in comprehensive observations (cf. 1926, *Biol. Zentralbl.*, 46: 405!). The following points must really be taken into consideration:

Our concepts and principles are deduced from experience accepting general logic, in other words, they are formed on the basis of facts, and wherever they are not in accordance with these facts, they have to undergo the modifications and get the complements required by the facts. The aim is not to elaborate a chosen formula for its own sake to the point that it ill-treats the facts, but to seek the verbal expression and interpretation that is in harmony with nature, even if a 'certain' uncertainty should prove inevitable. Concepts and principles of methodology are tools that need to be prepared appropriately!

It is a fact that normal ontogenesis reveals a certain liberty in the choice of the material from which some anlagen are built, so far as that material is *unformed* with regard to the parts to be differentiated. In particular if a number of equivalent form elements are available, it appears that the ontogenetic plan is not necessarily bound to choose one particular element when one is needed for a specific role. Instead it can pass, by steps, from one to the next, no matter which number the respective element holds in the strict bauplan of the essential preliminary stage, i.e. which exact position it has among its equals (cf. Goodrich, 1913; Kingsley, 1926).

Indeed the organism generates multiple form elements of the same kind (especially cells, but also multicellular differentiations) in highly variable numbers, and nobody would have the idea to homologize individual hairs on the head of one person with individual hairs on the head of another person. It is meaningful that the capacity to divide is proper to the ultimate and penultimate elements of all organizations. This leads us to the following principle (cf. 1926, *Biol. Zentralbl.*, Vol. 46, p. 409, p. 417):

Whenever single, structurally and positionally equivalent anlagen (cells, form elements) subsequently acquire special relationships with regard to the totality of the other parts, and take on a specific form in different organisms, the parts thus formed are to be considered homologous with regard to the whole, independently of the individual homologies of the respective original anlagen of the plan.

The occurrence of multiple formations in animals has even more significant consequences for homology theory: whenever such apparently isopotential parts attain higher complexity, the resulting organs must show identical bauplans that are comparable to one another, much like different animals among each other. We call them "homonomous" (loc. cit., p. 410) and recognize (e.g. in the hand and the foot) homologous parts and homologous stages during their development, and we realize that in the general framework of development they behave more or less like forms that are

similar in terms of their bauplan, which appear one after the other (Textfig. 1) as
 13 derivations of a germinal line, i.e. of an uninterrupted sequence of cell generations. Apparently there are *general, inner conditions* under which *similar (in terms of bauplan)* forms are generated (with or without the participation of outer conditions) as variants within such a framework.

Thus ontogenesis in several ways links up different and similar bauplans of living construction and therefore is the starting point for considerations and interpretations of the mutual relationships between such bauplans, even where no direct access to them is available for study. To *serially assemble forms with similar bauplans* and to explore the conceivable *modification (metamorphosis)* of plant and animal species through such series, must have been an early aspiration rather than just play to the searching human mind, as a source of comprehensive knowledge and deep insight into nature; the various possibilities to arrive at such serial arrangements indeed generated—long before the emergence of phylogenetic theory—the idea that all species are orderly related through stepwise modification (Galenus, Linné, Bonnet).

Moreover, for a science dealing with regularity concepts, the possibility that natural categories of organs and species can be conceived in relation to common ancestors could be deduced from the observed fact that ontogeneses with similar bauplans resemble each other more closely during early stages, and that different adult organs often start from a *generalized form of anlage*. This fact had an essential part in the emergence of the *type* concept in the writing of Goethe and Vicqu d'azyr, and of the more widely accepted concept of the *norm of formation*, which had been vaguely foreseen by earlier morphologists (Severino).

The *concept of type* is indispensable even today. It represents the *figurative norm of development* (form creation), and in a broader sense also the norms of behavior (function) and environmental relation (adaptation), *in the living individual* and in its *components*, and also with regard to natural *subspecies, species* and *greater entities* of the natural system.

The application of the type concept gives us a much more complete, perceptual and natural comprehension of the similarity relations than those formulated earlier (bauplan, ontogenetic plan, homology, metamorphosis, diagnosis), but the latter have to precede for logical reasons. In particular, the conceptual structure of the natural system based on simple diagnoses is partly improved by the type concept, but partly also made more transparent as it were. By its application the mere similarity of plan

expressed in the diagnoses is made more meaningful as an actual form relationship, the mere reference to the system (p. 10) becomes a systematic connection.

14 *Form relationship* here means typical similarity of development (form creation).

Typical similarity is the congruence of several body parts or whole organisms in terms of construction (development), behavior (function) and environmental relation (adaptation), permitting *reference to a common type* from which the variants can be derived *via* observed or supposed *intermediary forms* that must be *natural*, in other words, they are *conceived* as (hypothetical) results of *metamorphosis*. This produces a well defined, but purely formal relation.

Successions of conceivable types such as those formulated in the first volume (pp. 79, 91, 110, 136, 487, 656) to characterize the greater groups thus take the place of the systematic successions of theoretical categories.

For *detection of the typical* in embryonic development, the same principles apply as defined for any part of systematic morphology (Vol. 1, pp. 18-25), the ontogenetic facts having played an essential role in that definition. But only now does the constructional type take on the meaning of a truly ontogenetic type, which can be described solely by a sequence of conceivable, normal stages.

In summary, *comparative embryology* is a *mainstay* of systematic-morphological perception, i.e. of a science leading the way to the comprehension of a coherent, *family tree-like connection of forms*, based on unbiased observations viewed in the framework of logic. Although this connection initially expresses formal relations existing only in idea, and although in general *only* the forms are directly recognizable, this connection requires a theoretical interpretation and thus becomes the *foundation of general phylogenetic theory* (Vol. 1, p. 5). The *system* then *expresses hypothetical history*, and its increasingly comprehensive understanding leads to an idea about the evolution of the organic world as a whole or at least of some of its major parts. Systematic relationships then appear as expressions of real evolutionary trees of species, and the types of larger categories appear as expressions of the stem species. The *ontogenetic type* (developmental norm) of a group is the *mental image* that we have to assume for the *ontogenesis of the ancestor of this group*.

This theoretical history deals with forms, bauplans and norms of formation, phrased as ideas and images. As soon as we have recourse to modern science of heredity, however, this history is again reinterpreted as the history of something dynamic, as the history of the "hereditary factors" (cf. Vol. 1, p. 29!). Actually observed ances-

tral lineages do not represent developments in a strict sense (p. 4). There is no morphological continuity between a father and his son other than that of the cell generations along germ lines. They are indeed carriers of a form, but not of the one we actually consider in a reconstructed phylogeny. The phases of the latter, i.e. the images of the ancestors, here can only be represented *in terms of their potency*. Their relation to the former is the same as the relation of the genotype to the phenotype. Real evolution, however, is *transformation of the hereditary factors*. Only by this transformation can ontogeneses have been modified step by step, under endless recurrence combined with gradual shifts and deviations corresponding to those by which the sum or character of genes has changed through time (cf. the so-called "biogenetic theory" of O. Hertwig.).

So far as the diversity of extant ontogeneses can show relations to past life forms, they have to be considered under this angle of vision; the common elements are then viewed as general, those occurring in isolation as special ancestral features, the whole being a gradually modified combination of elements of different respective age and different morphological, physiological and ecological relation (cf. 1923, p. 387....).

2. On the Law of Conservative Preliminary Stages or the So-called “Fundamental Law of Biogenetics”

I

Although we find it highly satisfactory to be able to follow the change of bauplans in the course of ontogeneses and to see the relationships between developmental modes similar in terms of form, and although the special knowledge thus acquired has already proved useful in its application to fossil forms (1922), the emphasis of our interest is on the *general biological* significance and aspires to widely comprehensive knowledge.

The comparative consideration of a number of complete ontogeneses and parts of other, related ontogeneses, and the systematic study of this diversity aims at analyzing the connections expressed, in popular form, in the so-called “biogenetic fundamental law”, namely in the sentence: “Ontogenesis is merely an abbreviated recapitulation of phylogenesis”.

The preliminary result of this study has already been presented in previous publications*, but without details of the factual support underlying the conclusions
16 reached. Moreover, the clarity and evenness of expression required by such an important subject was not yet reached in many parts of these earlier presentations. Certain recent statements of colleagues indicate indeed that many misconceptions continue to

*Cf. 1913, 1917, 1920, 1921 (Vol. 1, pp. 3-35), 1925 (Zurich), 1926 (*Biologisches Zentralblatt*)

exist, so that a renewed consideration of the subject should not be superfluous. This reconsideration can have *full effect* only here, i.e. in close connection with an *organized estate* of newly-gained *factual fundamentals*.

There is no doubt that some truth is hidden in Ernst Haeckel's above-mentioned formula, at least in rough approximation; this partly explains its suggestive effect. On the other hand, something seems questionable with a "fundamental law" that makes an actually observed process (ontogenesis) dependent upon a hypothetical-problematic process (phylogenesis); especially when the relation between these (essentially different) processes is supposed to be simply a "direct causal nexus" entailing a "recapitulation" of the one by the other. That such a picturesque vagueness in the presentation of the most comprehensive relationships has been tolerated by so many biologists is very questionable indeed and certainly indicates the necessity of serious reflection.

We have to raise the question: "Are there real connections between the historical generation of species and the respective types of their present development; and if so: what connections?". Or, in a more restricted formulation: "Are the ontogenetic steps (stages) really congruent in terms of structure and sequence with *recognizable* phylogenetic steps? If so, in which way, to what degree, within what limits, and by the effect of which real connections?". Answering this complex of questions is not possible by simply invoking some textbook ideas. It is well known that during the development of animals certain apparently archaic or primitive features are formed; however, scientific interpretation of these facts in the sense of Haeckel requires three things: 1. precise knowledge of the respective ontogenesis and comprehension of its *real*, present conditioning; 2. secure knowledge of the *process*, or of the steps of the phylogenesis, i.e. of the generation of the species considered; 3. insight into the real *dependence* of a given ontogenesis upon the continuity of the life process throughout ancestral lineages.

This raises problems among the most general and most difficult of biology, and our question would appear unsolvable; if there were not an indirect way to comprehend the facts in an unambiguous context from which a reliable, though less sonorous, answer can be derived.

We can describe an individual ontogenesis, but we are utterly unable to describe
17 in an analytically explanatory manner the machinery of the factors responsible for it. Moreover, we know tons of fossils, but we cannot trace backwards a single species through continuous phyletic series far enough to merely permit a rough empirical approximation of the parallel between ontogenetic stages and phylogenetic steps. The

laws of heredity certainly provide us with a fair insight into the "mendelian" and "pendulous" behavior of single (generally rather unimportant) characters; but the dynamics of the conservation of the type as a whole and its capacity to change in the course of long descendant lineages remains largely incomprehensible. The recapitulation invoked by the phylogeneticists was indeed based on a vague similarity between some foggy contours or isolated details of embryonic states and some fanciful, arbitrary ancestral images, rather than on clearly perceived regularities underlying the comprehensive laws of organic form creation.

And yet, some reliable statements can be made in this sense, i.e. questions and answers can be brought to a level above purely speculative discussion and some positive, general knowledge can be gained without removing mountains, that is without claiming to resolve once and for ever the fundamental problems of biology.

II

The most general, and in its consequences most significant, fact derived from unbiased comparison of ontogeneses is this: *the preliminary stages of homologous formations, i.e. the beginnings of morphogeneses, are always much more similar than they appear during their later phases.* In many instances this is even true (with a not too critical observer) for whole embryos. It is indeed surprising that early stages of *Octopus* and *Argonauta* are almost identical, except for the yolk mass (Pls. 27 and 33); and it is even more striking that early embryos of *Sepia* and *Loligo*, which are representatives of different suborders, are so much alike; and so on.

This strong similarity of very early states is important not only as a foundation for the "morphological primacy of ontogenetic precedence" (Vol. 1, p. 19), it also facilitates (even for the unmethodical observer) obtaining an image of the *primary type*, i.e. of the ontogenetic norm valid within certain form ranges. As Johannes Müller already remarked, the young stages, being close to one another, are also close to the general type, the latter being indeed defined based on these conditions. A morphologically trained eye cannot avoid seeing a certain image of the regular postembryonic juvenile form of a teuthoid squid when comparing textfigures 68 and 71-77; this image appears
 18 almost automatically from the general appearance, and even more so when individual

parts such as the fins, the arm rudiments or the eyes are viewed. They pass (somewhat earlier in certain instances, somewhat later in others) through the same states and build their development on entirely equal anlagen, as will be seen later.

Given that some animals change only little during later development and thus stay relatively close to the typical embryonic states, whereas others undergo great modifications that may even totally obscure the primary bauplan, it is obvious that the *embryos* or larvae of those having changed greatly during later development *resemble the adult forms* of those animals which have undergone only little modification during advanced developmental stages. This observation has drawn considerable attention already at the end of the eighteenth century. Much more than the preliminary and rudimentary stages, it appeared to reflect an enigmatic relationship between the essential features of wide systematic ranges; a relationship bringing into focus the general order of nature underlying organic diversity. This order had to be recognized as gradual once the organizational level, which increases in the course of ontogenetic development, was viewed in parallel with the apparently natural sequence of systematic categories termed "animal series".

This refers primarily to the series of vertebrate classes and their relation to the "worms", but remember the concept of systematic gradation discussed on pages 3 and 10! Probably Kiehmeyer (ca. 1790) was the first to formulate the theory according to which the "higher" animals have to pass "through the lower classes" during their ontogenesis. The idea of a "parallel between the individual development of higher animals and the animal series" was presented in greater detail by Meckel (1811). However, the real situation was seized much more clearly by K.E. v. Baer whose considerations remain conclusive in many respects. I therefore quote the most important sentences from his principal work of 1828:

Page 220: "The embryos of vertebrates do not pass in their development through (known) definitive animal forms". Pages 221-222: "The basic type appears first, followed by increasingly subordinate variations". "Thus the more special type is formed from a more general one". "The more different two animal forms are, the farther one has to go back in their ontogenies to find congruence".

Page 223: "At first appearance perhaps all animals are equal being simply hollow spheres" (!) Page 224: "The common features of a greater animal group are formed earlier in the embryo than the special features". "From the most general of form conditions the less general is achieved, and so on, until the most special appears". "Each

19 embryo of a given animal form becomes increasingly different from other forms rather than passing through them. So essentially the embryo of a higher animal form never equals a different animal form but only its embryo". (Wrong possessive pronoun in original text.)

"Since simple animal forms do not develop very far beyond their embryonic condition, they keep a certain similarity to embryos of higher animal forms. So this similarity is ... not the causation of higher animal development; it is simply a consequence of the organization in lower animals" (!). Page 225: "With regard to the organizational type, the development of the embryo behaves as if it passed through the animal kingdom using the *analytical method* of the French systematists, always moving away from the related forms and, at the same time, progressing from the lower grade of inner organization to the next higher". (This statement is graphically illustrated with a plate arranged in a way similar to an identification key!) "The representation can only be very incomplete since the study has barely started for most animal forms". "Once the vertebrate type appears, the embryo is all vertebrate, without special features". "Afterwards a separation occurs" (in the mutual relationship of ontogenetic plans compared with one another): "Some form gills but no urinary sac, in others the gill slits fuse and a urinary sac is formed" (Anamnia and Amniota!). "In a bird the special features of the family and of the genus appear progressively; likewise in a mammal. A hog and a dog are very similar at the outset".

At some later point, in one of his published addresses (precise reference not available), v. Baer makes the following statement: "In its earliest state each organism shares most of its features with all the other organisms in their earliest state; at a later stage it structurally resembles a smaller number of organisms at corresponding stages; at each subsequent stage new features appear and progressively distinguish the embryo from others which it resembled previously,—hence the group of similar embryos becomes progressively smaller,—and so the class of similar forms finally shrinks to the species to which the embryo belongs".

20 Thus K.E. v. Baer clearly recognized that no adult animal forms are passed through, but that *regular congruences* exist between embryos, and between adults (in our terminology this reads more precisely: between *homologous stages*). This represents a very close approximation to the facts which was subsequently disregarded in many instances; in particular it reduces any foggy relationships, which were more felt than recognized, to fairly incisive, unambiguous (!) similarities.

III

But even this critical conception requires some further precision of limiting nature: the increasing degree of generality observed when going back to the outset of ontogenesis does not necessarily concern the stages in their entirety, but only their individual, more or less independent parts (morphogeneses). At a given time, the latter may have reached quite different stages of the systematic differentiation, as I have pointed out in 1920 (pp. 13-15), some appearing very premature while others appear equally belated. There is no comprehensive rule available about what general features co-occur at a given stage; the real regularity underlying the relationships considered here is concerned with the sequence in time, and in particular with the question of *how the occurring features are, in terms of their systematic generality or speciality, related to the features they entail*. This is the essential insight in this context that I have gained through my comparative studies, leading beyond the definitions given by K.E. v. Baer.

Any embryologist knows that the embryonic forms occurring within a well-defined group may differ in terms of their composition of elements; so quite often, along with searching for features supposed to have occurred in ancestors, one may not in vain search for features still occurring in systematically close relatives. There is absolutely no compulsory embryonic form valid for all teleosts or amphibians or mammals or great apes; in fact each specific type shows some *particular features* already at *early stages*—incidentally this objection was already put forward by contemporaries of K.E. v. Baer.

Thus the regularity we are seeking here and whose occurrences we try to confine to something amenable to precise definition is only concerned with the individual form elements of given stages in their *relationship to the resulting* formations. i.e. to those directly and really *ensuing* from them. Compared to the ensuing formations, they always show an increasingly general character when viewed retrogressively towards the beginning of development.

There are some cases, however, in which even this rule *seems* to be violated: advanced (larval) stages of oegopsid squids (cf. Vol. 1. Pl. 4, Fig. 3; see also below the
21 Textfigs. 76 and 77 compared to 68) are very close to the type of loliginid larvae, whereas the embryos and the *youngest larvae* (cf. Pls. 8 and 9 with 3) appear *strikingly*

different. However, a more detailed comparison provides the following adjustment: the different storage of the yolk mass and its smaller volume in oegopsids (cf. chapter 4) conditions the peculiar *overall habit* of the early stages; this implies a *displacement of rudiments in relation to one another* compared to the normal situation but does not cause substantial deviations in these rudiments.

This peculiarity of some early stages is relatively unimportant for the course of differentiation of individual parts and their potential features or general correlation, if we disregard the distension of certain organ connections and the contraction of others. One can even demonstrate experimentally that a modification of surface tensions in the embryo pushes one type (the *Loligo* form) in the direction of the other (oegopsid form); in many respects the inner yolk indeed has as a *purely mechanical action* in the achievement of the embryonic form. (This does not exclude the possibility for the embryo to realize special adaptations related to the yolk mass, the latter perhaps providing specific stimuli for their formation.)

Often such irregularities are simply suggested by comparison of differentiations that are not really comparable. Thus one observes fairly different cleavage patterns in octopods and decapods (Pls. 1 and 24), whereas the later embryos are again typically rather similar to one another (Pls. 3, 4 and 27). Here one has to consider that the generation of certain outline forms and even finer anatomical similarities and homologies do *not depend upon an identical cell mosaic* (p. 12). On the contrary, any part of the embryo can be made of numerous or only few cells, and its form is not determined just mechanically by the individual building blocks.

We are here deliberately introducing a new aspect into our discussion, namely the *causal viewpoint*. Long experience has taught us that we cannot compare forms without considering their real significance in the context of *effectiveness*, not even when aiming only at a *systematic order* of observed forms. In fact we find that the greater similarity of earlier ontogenetic features is expressed in particular in those characters that can be supposed to provide the necessary conditions for later states; in other words, this expression reflects the relative importance of a character for the sequential process of ontogenesis.—In any event, the range of validity of v. Baer's rules (p. 20) has to be restricted if it is to be made stringent.

22 We can nevertheless avoid assigning to a dynamic developmental analysis the ultimate criteria relevant for a purely ordinal arrangement of form elements, if we consider the following point: *the rules of form change cannot be valid for the shapeless* (cf. p.

12) but only for the change of existing from. Moreover, the principals of order in organ formations are concerned with the constitution of *formed rudiments*, not with any disposition of formative material one may imagine. The sacrum of a vertebrate is not established by the mere presence of the vertebrae from which it is built, no more than any organ is established by the mere presence of the cells that will make it! This is relevant for the general concept of anlage, not for the special observations in the course of a comparison (cf. 1925, Zurich, p. 238). Even properly ordered *material* has to be considered shapeless in relation to later, specially integrated *parts* that are formed from that material. In particular, the mosaic of cells in an epithelial complex (blastoderm, germ layers) has to be viewed as indifferent with regard to the parts produced from these cells.

There are rather rare instances in which it is legitimate to talk about a *structure of homologous cells* (in which bauplan, type and developmental determination are strictly dependent on the cell arrangement). This should not be taken as a further curtailment of v. Baer's theses; it is merely a necessary conceptual specification of the aforesaid.

There is no need in this context for a special discussion of *embryonic and larval organs*. They conform to the general rule. The concept underlying these designations requires some critical considerations, however. We are indeed accustomed to take account only of the most prominent among the transitory parts of a developing organism. A morphological definition must in fact be applicable to *all* early transitory parts including those (very numerous) which are of small dimension and thus very inconspicuous within the form as a whole.

Minor embryonic and larval organs can still strikingly modify the overall aspect and behavior of an organism, e.g. by tying parts that are normally separate or by separating normally tied ones or by closing natural openings. A coarse-grained picture gives the impression that the ostensibly atypical rudiments deviate at early stages from the general bauplan, to approach it again at later stages, i.e. when these rather easily overlooked organs disappear (see e.g. end of chapter 7 on the proboscis of ommastrephid larvae!). A detailed comparison between related forms, however, allows one to readily distinguish these special differentiations that occur in some (cf. pp. 8-9), and it shows that these differentiations (and the parts masked by them) follow the normal course, and that the relatively general nature of the preliminary states is never reversed to its opposite.

23 Before rephrasing the results of objective-systematic comparison of noted facts according to a theoretical-historical interpretation, we can already attempt a gener-

al formulation of the observed regularity: *As far as (i.e. in those parts and properties in which) the formative conditions of an ontogenetic stage physically produce (i.e. enter into and thus co-determine) the conditions of the following stage, they have (in a systematic perspective) an equal or higher degree of generality than the latter.*—This is always valid for a given partial state in relation to the immediately resulting one.

This does not imply any definite statement about the *degree* of specialisation from one stage to the next. In fact there is no exact measure for that, and in the sense of systematic particularity, progress can indeed be nil. It is absolutely conceivable and not in contradiction with the above rule that a given preliminary stage has no distinctly higher generality than the following stage.

This specification is necessary to precisely define the meaning of the sentence. An additional step makes it into a *methodical principle* of pure (i.e. not yet genealogically interpreted) systematics: *As far as (i.e. in those parts and properties in which) the formative conditions of an ontogenetic stage physically produce (i.e. "enter into" and thus co-determine) the conditions of the following stage, systematic consideration has to assign an equal or higher degree of generality to them than to the latter.*

A further empirical sentence, which cannot be analyzed here in detail, would be: *As far as ... the formative conditions of an ontogenetic stage assist in the physical production of the conditions of the following stage, they often indicate a particular congruence with the conditions of paleontologically older groups.* Examples in the present work are: 1. The reminiscences (we will see a lot of them) of the early developmental stages of cephalopods evoking *Nautilus* or the older chambered shelled mollusks. 2. The reminiscences of embryos and larvae of extant teuthoids and sepioids evoking conditions of the fossil belemnites, especially with regard to the relation between the muscular mantle and the cone part of the shell.—This point
24 could be illustrated with much more numerous examples from the morphology of vertebrates.

If one wants to apply the knowledge thus gained to the old theory of parallels, or to Haeckel's *formula* of the "*triple parallel of the systematic, embryological and paleontological developmental series*", it can be done with the following three sentences:

1. *As far as formative conditions of different degrees of generality are physically resulting from one another in the course of ontogenesis, they succeed one another*

in the same sequence, i.e. with the same successive numbers, as the types in the series of systematic preliminary stages in which they occur at homologous stages.

2. *As far as paleontological records allow one to judge, the systematic preliminary stages of an extant species appear historically in the same sequence, i.e. with parallel numbering, as in the system. (See 1926, Biol. Zentralblatt, 46: 205...!).*

3. *As far as an ontogenesis shows form states that are morphologically congruent with presumed or actually observed rudimentary states of fossil forms, they appear in the same sequence as in geological history, provided the respective complex of forms is sufficiently well represented (abundant) in the fossil record.*

IV

The “fundamental law of biogenetics”, which was given a suggestive formulation and a sonorous name by Ernst Haeckel (1866) following the statements of Fritz Müller (1864), is merely a translation of the old, unfortunately never clarified, theory of the “parallel between ontogenesis and animal series” (p. 18) into a descent-hypothetical phraseology (cf. Vol. 1, p. 26). The correction suggested by K.E.v. Baer (p. 19) was first taken into consideration by F. Müller but subsequently neglected, while E. Haeckel ignored it entirely. The resulting, striking inconsistency between the “law” and the facts was pasted over with the “falsification” already proposed by F. Müller for which Haeckel coined the term “caenogenesis”, in contrast to which he used “palingenesis” to designate the faithful recapitulation of the “series of ancestors in summary”, something that is in fact never observed. The actual meaning of this concept is derived from the idea that a mysterious reminiscence of phyletic history as a whole survives in the germ and induces its behavior.

In contrast, F. Müller had comprehended the process in a clear and sober manner: the continuous development of a phylum is generally achieved in that descendants having attained the parental form do not stop but *proceed beyond that form*. Ontogenesis thus gradually grows longer at its end (Textfig. 2), and the formerly adult ancestral forms become merely transitional stages. This idea is very attractive; yet it is wrong!

As has been shown already by K.E. v. Baer, ontogenetic stages in general do not represent adult stages of related, but lower, animals; instead they correspond, often in



Textfigure 2.—A graph representing the understanding of morphological relationships between the ontogeneses of an ancestral series and their phylogenetic modifications, as originally accepted by the “biogenetic fundamental law” (from Naef, 1917, p. 11). The dark base line represents the continuity of development proceeding from ovum to ovum.—A-A₁-A₂ etc. would thus be (very widely separated) egg cells of the stem line. The ascending lines represent the ontogenetic paths which become increasingly complicated by the addition of further modifications to the end of development, the stages of previous ontogeneses being recapitulated. The increasing meandering of these lines visualizes the deviations (called cenogeneses) from the primary developmental course. Homologous stages bear the same letters, the added index expressing the change of prospective potencies.—This view gives only a very imprecise and ultimately confusing interpretation of development in closely related organisms.

a strikingly complete way, to homologous transitional stages of such lower relatives. As an example, one may consider the correspondence between the larvae of archaic fishes, especially Dipnoi and Crossopterygii, and those of amphibians! Or the similarity of 20 day old human embryos with corresponding stages of sharks and rays! The adult stage of a low grade in the animal series is in no way “repeated” by a higher one, but it is *replaced* with a homologous, but modified, form state; if it is not skipped altogether as can be observed in complete *paedogenesis* but also frequently in certain parts of derived animal forms. The arrest of juvenile characters is one of the most common forms of metamorphosis (p. 13) of various animal types and corresponds phylogenetically to an extremely obvious, highly likely process. For if juveniles have to be successful anyway in the struggle for existence, their ecological proof is relatively secure in advance as it were, in case their further modification is omitted.—Of course this kind of modification of types will in many cases be very difficult or even impossible to demonstrate! (Cf. final section.)

In any event it plays a particular role in the *atrophy* of organs, for which numerous examples were given in Volume 1. Here I will mention only a few especially noteworthy cases: 1. the strongly stunted condition of the buccal lappets (buccal arm rudiments) in many decapods (on such a rudiment there can be up to 13 suckers formed

sequentially, whereas in most species there are only few or no suckers). 2. the rudimentation of the phragmocone, which had more than one hundred chambers in some belemnoids, whereas in *Xiphoteuthis* there were only few, and in the teuthoids, sepiolids, idiosepiids and octopods there are in general no septa at all. 3. the atrophy of the proostracum in sepiids, idiosepiids, sepiolids, spirulids and octopods.

In contrast, *nothing* appears in morphological gradations that would have been *added* to the end of a typical ontogenesis; when this end shows a special degree of differentiation in a derived form, it always turns out to be the homolog of a differentiation present in the type though in simpler form.

F. Müller as well as E. Haeckel of course realized that the series of stages of a given ontogenesis is very different from an imagined series of ancestors; but instead of testing their basic idea (recapitulation of ancestors), they casually explained the difference by a secondary simplification and blurring of the process. According to this scheme, even the "palingenetic" ontogenesis is only a "summary" of phylogeny, the latter being repeated only "in general traits". With this vague shift of the primary conception they avoided the contradictions of the "law" without getting closer to the facts. The retreat into vagueness is even more obvious in the assumption of "caenogenetic" development, i.e. of actual "*falsification*" of the phylogenetic record by introduction of form elements that cannot have existed in adult ancestors since they could only serve during ontogenetic stages.

The concept of *caenogenesis* has rubber-like extensibility and of course permits any deviation from the "fundamental law"; close scrutiny reveals it as a petition in bankruptcy of that law. Apart from the larval and embryonic organs it "explains" all those cases in which early stages of related animals are more different from one another, hence also from the primitive form, than later ones; admitting faithful recapitulation, one would thus have to assume that different ways, i.e. different lineages of descent, would have led phylogeny to the same destination. Some morphologists indulge in assuming this quite frequently. Once the "law" has lost all footing, it simply becomes a matter of "feeling" for a researcher whether or not something has to be considered primary.

V

We have to cope with the question why, despite all criticisms, the “biogenetic fundamental law” has remained in people’s minds and in the textbooks, and we will find the explanation in an often quite incredible *neglect of logical thinking*, in which biological sciences indulged for a long time in favoring an uncritical consideration of the immense “material” of facts. The living object appeared interesting and meaningful even without any intellectual effort, and it proved attractive even to the careless observer.—On the other side, the thousandfold recurrence of the observable fact that developmental stages of higher animals resembled conspicuously those of lower relatives, and even their adult stages required a comprehensive formulation and explanation based on a serious consideration of the historical past.

This requirement was specially emphasized by the following fact: Whereas in some instances the rudimentary and transitional stages appear as an appropriate preparation for subsequent stages, other instances are about as numerous where development makes obvious detours and produces parts, the *ecological insignificance* of which is demonstrated by their rapid degeneration, or their physiological uselessness is illustrated by their immediate modification. For example, there is no reason other than a *historical basis* for the embryonic differentiation of dental rudiments in whales devoid of teeth when adult, or for the formation of a little shell in the embryos of unshelled gastropods, or for the derivation of the rudiment of the cornea in our dibranchiate cephalopods from extensions of the arms (chapter 2). What was needed was a formula like the one proposed by Haeckel to summarize and interpret these facts; such a formula was difficult to avoid although the informed person was aware of its insufficiency. A Russian proverb says: “If no fish is available, the crab can become a fish!”

28 The often quite uncritical criticisms generally enhanced the vagueness of the conception. The “fundamental law” was degraded to become a “rule” or was evasively called a “principle” in order to provide a pleasant uncertainty. Keibel calls it a “heuristic principle”, by which at least its methodological side is characterized. However, the really well-founded principles of science have to be as unambiguous as the laws of nature; in trying to grasp both of them, one should make every effort to attain the highest possible precision.

The post-Darwinian morphology indeed rested on quite peculiar foundations, for which Haeckel can again be cited as a witness. In his "General Morphology" (1866) and—forty years later—in his "Principles of General Morphology" (1906, p. 337) he states: "The theory of selection and the causally ensuing theory of derivation are physiological theories that form the indispensable foundation for the morphology of organisms". Furthermore, he asserts (p. 338) that "the common derivation of related organisms from most simple ancestors is the only existing idea explaining in a mechanical way the development of organisms and hence the entire conditions of form. There is no other explanation."

This, however, means placing the cart before the horses and from the outset forbids a solution for the most general problems: The foundation of systematic morphology as a critical science dealing with natural things is made of the facts of organic form creation and of the general principles of logic by which man approaches the natural order. The aspiration of intellectual translation of organic diversity in the natural system (p. 9) should be unbiased and unburdened of theories when coping with the facts and should try to answer the purpose with the general means of cognition. It then becomes evident that systematic morphology is the basis for both general and specific descendancy theories, rather than the other way round. As to selection theory, it does not belong here to begin with. From the facts of morphology alone it cannot yet be deduced; it is only an hypothesis dealing with dynamic aspects complementary to the systematic foundations of the general theory of derivation—it is still tentative indeed (cf. 1926, *Biol. Zentralbl.*, p. 313).

VI

In the preceding sections (pp. 18-25) we have shown that the relationships expressed by the "biogenetic fundamental law" can to a large extent be grasped and clarified without phylogenetic theory. If we attempt to apply the general theory, it will be useful to start from formulating it: *We observe that the diversity of organic species*
 29 *is of such nature and distribution in time and space that one can assume each natural group has been formed from a single ancestral species by gradual modification of heritable features.*

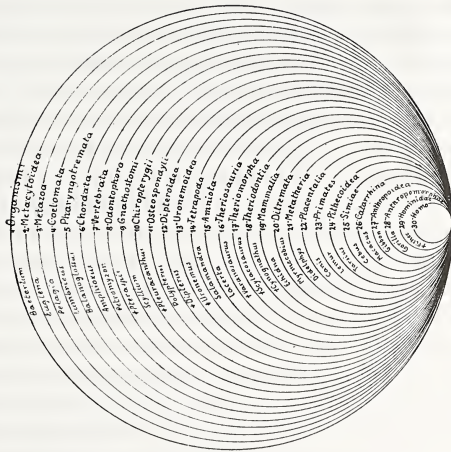
In a more general formulation: We find the diversity of organic forms to be of such nature and relationships and distributed in space and time *as if the systematically general and morphologically primary features were indeed the genetically primitive*, and as if the visually evident *type* of morphological and systematic categories corresponded to the image of the respective *ancestral form*. How far this is not in contradiction with the facts but can be deduced from them is a general question that cannot be dealt with here, and at this point we must refrain from actually formulating a corresponding principle. However, in this context we can nevertheless coin a special statement based on the above-mentioned observations:

So far as the formative conditions of an ontogenetic stage are physically generating the conditions of the subsequent stage (cf. p. 21), they are more primitive than the latter in phylogenetic terms.

K.E. v. Baer himself stated: "Usual reasoning wants it that anything appearing very early in development is a heritage from the earliest ancestors". In actual fact this formula was not at all usual for his time; it represented a considerably increased sharpness in the manner of drawing phylogenetic conclusions from ontogeny. This sharpness reflects his correction (p. 19) on the 'concept of parallelism', which was not taken into account by Haeckel—much to the disadvantage of critical phylogenetics.

In the translation of this old concept into the language of descendancy theory, i.e. into the 'biogenetic fundamental law', the *ambiguity of the conception of an animal series*, which already in idealistic morphology had prevented a solid clarification of relationships, again took its toll. If we aim here at such a clarification, we have to begin by filling this gap, i.e. by replacing the concept of animal series by an unambiguous, unbiased concept; this purpose is served by the concept of *systematic gradation* as coined above (p. 10). For each species or subspecies under study, this concept can be visualized by a system of excentrically arranged circles, which express the order of relatives through a stepwise enlargement of the system (Textfig. 3). In this representation, the series representing two sorts of systematic categories are very distinct, namely the series of stepwise *annexed* groups, and the series formed for their successive *inclusion*.

The first series generally contains relatively small units, so that in principle they can be represented by genera (as is done in the present diagram), which are not surrounded each by a special circle. This series thus becomes rather tangible, and a fanciful and hasty morphology devoid of critical insight has always considered phylogeny to be embodied in such a combination.



Textfigure 3.—Schematic presentation of the concept of “systematic gradation”, by which the position of any species is determined within the context of a natural system (p. 10), and which provides hints about the phylogenetic process. Here the concept is visualized with special reference to the position of humans. The increasingly inclusive, nested groups of the natural system are given, step by step, up to the group of organisms in general, with the respective group names, and numbered (backwards) starting from the latter group. The circles themselves visualize the diagnoses or definitions, which determine the limits of the sectors considered within the system.

Each circle includes, in addition to the next narrower one, an individual group representative (excluding *Homo sapiens*); for reasons of readability, these representatives are not given special circles (From Naef, 1926, Erg. Fortschr. Zool., Vol. 7, p. 28).

The logic of the general theory of derivation requires something different, however (cf. 1925, Zurich, pp. 234-240!): If, as we must suppose, the natural system is the expression of the grades through which the extant organisms have *passed*, this expression must (for each species considered) be based on those groups to which the species considered *belongs* in a stepwise extension or reduction. In Textfigure 3, which visualizes the systematic grades leading to man (taken as an example), this series is emphasized by naming and numbering the circles.

31 Similarly, one can express the systematic-phylogenetic position of *Sepia officinalis* by the following formation of groups, of which only the first four are congruent with the grades leading to man:

1. Organismi, 2. Metacytoidea, 3. Metazoa, 4. Coelomata, 5. Eutrochaeta (cf. chapter 1), 6. Mollusca, 7. Conchifera, 8. Cephalopoda, 9. Dibranchiata, 10. Decapoda, 11. Sepioidea, 12. Spirulirostroidea, 13. Spirulirostrinoidea (cf. chapters 8-9), 14. Sepiidae, 15. Sepiinae, 16. *Sepia*, 17. *S. officinalis*.

A perceptual *representation of phylogenesis* results from the *systematic gradation* if we consider for each group of this gradation *the respective morphological norm* or the primary developmental type; when talking about recapitulation of phylogeny as a known process (p. 17), strictly speaking one can only mean the passage through the observed series of developmental types, which appears as a series of ancestors in the interpretation proposed by the theory of derivation (p. 14). Indeed this is the only well-founded knowledge at our disposal!! It is of course quite unthinkable that in ontogenesis man passes through all the successive form states typical for the 29 preliminary stages, and it is also impossible in principle to place the ontogenesis of man in parallel with such a (still very incomplete) phylogeny; for the latter can in fact be represented morphologically only as a sequence of ideal (reconstructed) ontogeneses.

The question therefore is: How is development in the ontogenesis of an extant animal related to the series (representing phylogeny) of typical developments in its preliminary systematic stages.

The vague concept of recapitulation cannot express this relationship in an appropriate and unambiguous manner, because ontogenesis recapitulates only itself, generation after generation (although apparently with somewhat limited fidelity); the idea of a stepwise terminal lengthening of ontogenesis as proposed by F. Müller was already rejected above. Such a process is never observed in the course of morphological series established according to the above scheme, although a *special case* of phylogenetic development exists in which the result mimicks relatively closely the above process (cf. below, p. 34).

We could well imagine, however, that e.g. man today develops through 29 *preliminary stages* whose sequence is congruent with *homologous* stages of the *preliminary systematic grades* leading up to man, and that all the other species undergo the same sort of development. To a certain degree of rough approach, this is really so, as pointed out already by K.E. v. Baer (p. 20). But with regard to such an idea, of course, 32 restrictions made in a purely systematic view remain valid as far as the degree of generality of preliminary states is concerned (p. 21).

Indeed, once the general features of natural groups are explained as common ancestral heritage by the theory of derivation (pp. 14 and 30), deviations at homologous

preliminary stages then prove that the ancestral heritage apparently has not remained unchanged, and if in certain individuals features of different degrees of generality coexist, this is evidence that modifications of these features occur at a different tempo, i.e. independently from one another. *Regularities* expressed in the *results* (as observed) can then be understood in the framework of *laws of causal connection* in ontogenesis, which we have to assess from their effects (!).

A law supposed to explain the phenomena discussed here can be concerned only with hindering of early or promotion of late ontogenetic stages in the course of a phylogenetic modification of the typical ontogeny, or with both together, at any rate something that can be expressed by a simple relationship. The *early stages* have to be *relatively conservative*, with the same definitions and limitations as explained earlier (pp. 21-25) with regard to the degree of generality of formations. So far as the early stages show a higher degree of generality in systematic terms than the later stages, one can explain this phenomenon under the assumption that the tempo of heritable modifications was lower for them than for the later stages, with the gradation actually observed. Thus we simply arrive at a translation of the sentence given in the upper part of p. 24 into a phylogenetic version, with the following words:

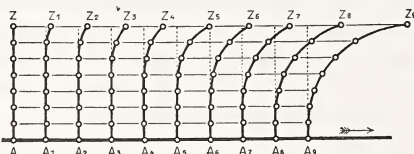
So far (i.e. in those parts and properties) as the formative conditions of an ontogenetic stage physically generate those of the subsequent stage (i.e. "turn into" them and thus co-condition them), they lag behind them more or less drastically during the phylogenetic modification of the typical ontogenesis, in other words, they are more conservative than the formative conditions of the subsequent stage.

Such a law, which represents a corollary to the general theory of derivation and thus is *theoretical* in nature, can underpin an explanation of the special relationships between ontogenetic and phylogenetic development.

We might call these relationships a *parallel* (in the sense of Meckel and Haeckel, 33 but with higher precision) between ontogenetic and phylogenetic *gradations of preliminary stages* at the level of an individuum. The former would then be represented by the sequence of individual developmental stages, the latter by the systematic gradation interpreted in terms of group genealogy. If the relation of ontogeneses to one another were as simple, general and regular as was surmised by K.E. v. Baer (p. 20), the term "parallel" would mean that the states of form arise in ontogenesis in exactly the same order (in other words, with *parallel numbering*) as in the series of ancestors, i.e. the oldest first, the younger always later. But since we have seen that this

condition does not entirely come true, we can make only a restricted statement on the matter:

So far as in the course of individual ontogenesis formative conditions of different phylogenetic age arise physically from one another, they follow one another in the same sequence, i.e. with parallel numbering, as do the ancestors in which they first appeared at homologous stages. The statements 2 and 3 given on p. 25 can of course be translated into a corresponding form of phylogenetic statement.



Textfigure 4.—(From Naef, 1917, p.29) Schematic presentation of the phylogenetic modification of morphogeneses according to the law of conservative preliminary stages. The basal line (A-A₁ etc.) has the same meaning as in Textfigure 1; but here the ascending lines represent only the partial developments (morphogeneses) that compose an ontogenesis; they are directly or indirectly connected to the germ line. In the course of phylogeny, the morphogenetic stages close to the rudiment change relatively little while those close to the end of ontogenesis change more markedly.

We believe that the above statements clarify a hitherto obscure state of affairs, but we are aware that this clarification could only be obtained by sacrificing much of an ostensibly comprehensive insight. This raises the question whether what is retained by our net of critical review is not too little. One will agree that a *sharply formulated criticism* provides more than a vague notion and paraphrase of a relationship could do, and yet the thought remains that there might be something other than what is expressed by the sober formula. Above all, the idea of the entirety of the individual (at all stages of its development) will arise and raise some hopes as to the possibility that after all this entirety were subject to a *more comprehensive law* of transformation than can be recognized from an analytical study of its parts.

Certain facts would seem to support this perspective: It is indeed undeniable that quite often the younger organism produces more general, in other words more ancient formations, the homonomes of which acquire an increasingly particular character later on. For example, the lobular lines in young ammonites are simple and approach the normal, later stage stepwise, according to certain rules. Thus these animals appear to have produced, *first ancient* and *later on* increasingly *modern* structures, suggesting a

corresponding modification of their entire nature in the course of their individual development (Cf. also 1917, p. 59).

It is quite clear, however, that this cannot be considered a general behavior of organisms. On the contrary there are hundreds of cases in which the *young germs*, larvae or animals, produce rather *peculiar structures* first that are later replaced by absolutely normal ones. The case mentioned above (like many similar cases) provides a very special aspect, however: The lobular lines and the septa to which they belong are not living parts of the organism, they are secretions of one and the same formative matrix. It is not the septa which undergo the problematic development, nor is it the animal as a whole that is concerned, but the organ only which produces the septa. (See Textfig. 26 where this organ is marked by hatching and given the number 4).

The *special case* of regular modification of ontogenesis in the course of phylogenesis, which may *simulate a recapitulation* of adult ancestors, can be characterized in the following way: If in the course of phylogeny juvenile stages undergo a progressive displacement or a cumulative complication of bauplan involving persistent, functional organs which participate in the open struggle for existence of the free-living animal, the resulting (derived) ontogenetic pattern *cannot* be conspicuously different from the picture of a series of adult ancestral forms. However, this observation does not change anything in the fact that generally terminal stages remain homologous to terminal states and transitional states remain homologous to transitional stages, respectively, and they correspondingly have to be deduced in phylogenetic terms, which is something that must arise more or less distinctly from the whole *co-ordination* within the ontogenetic pattern (Cf. below, p. 39).

VIII

Haeckel gave his sentence the title of a law, although the form does not justify clearly this characterization anywhere, and we have followed him in this respect. A *natural law* must, however, express the real dependence of phenomena on one another in a well-defined, unambiguous form, following the formula: "If (so far as) this is like this, that is (becomes) like that".

That our sentence is correct can be seen in the context of a huge matter of fact, which is embraced here only conceptually and which may need a further interpretation

if the terms used were given a different meaning. We can indeed have them in variations: I have used earlier (1913, 1917) the term morphogenesis (p. 8), to express the rather strict relationship between preceding and subsequent stages, and to exclude the widely accepted, yet erroneous opinion according to which any preceding state as such, just for its being preceding, must be phylogenetically conservative. Using the concept of morphogenesis, one can give the following formulation:

Preceding stages of a morphogenesis are, with regard to their bauplan, phylogenetically more or less markedly conservative compared to subsequent ones.

Here the specification "more or less markedly" of course means that one cannot give an absolute definition of the degree of phylogenetic lag in preceding stages compared to subsequent stages (cf. p. 24), but a relative one only. A valid general statement therefore can only be that preceding stages cannot be more progressive than the subsequent ones.

The *law-like nature* of our sentence stems from the recognition that this phenomenon is an inevitable result of a *connection of effects*. We are dealing here only with a *statistical law*, i.e. a law which ultimately deals with an unequal probability for the occurrence of numerous, largely optional events. Doubtless phylogenesis is made of innumerable individual events that occur over an extremely long time. The question then is whether an *unequal probability* of such events is *determined by the process of ontogenetic development*, which here forms the correlative system for the process of phylogenetic development.

This is indeed the case: For if we consider development (p. 4) as a cumulative process, it is inevitable that the typical modification of a stage cannot occur in isolation but must also concern the subsequent stages. If the construction of one stage is shifted by this modification, initial conditions for subsequent processes are also modified, so that the effect obtained is at least conserved during these processes, but often such an effect is even automatically enhanced. The extent of the ultimate effect of a modification that occurred at an early stage is therefore likely to exceed the initial amount (which cannot be quantified in a generally valid manner), unless particular countereffects slow down the process later on. We of course assume that such modifications result from modifications of hereditary factors, in other words that the apparatus of the "genes" is involved, rather than that the living germ would simply have to undergo and compensate perturbations acting from outside. For only genotypic shifting can explain the phylogenetic connexions.

Given these considerations, the general probability that such a modification of a single phase disturbs the *harmonious process* of development must differ for the various stages: it must increase towards the beginning and decrease towards the end of the ontogenesis. A modification of the terminal stage concerns only that very state (i.e. must be acceptable for the terminal stage itself); it cannot have any effect on other stages. Modification of earlier stages, however, means at least shifting the foundation upon which the whole edifice will have to be constructed, perhaps even more than that: For if we consider the germ as the acting subject in its own elaboration, as much as it is its object, it appears that *any viable* modification of notable extent in early phases must be *extremely unlikely*.

At any rate one has to consider that early stages of a developmental process, viewed in the context of developmental mechanics, carry an enormous burden since in addition to insuring their own life they also have to generate all the subsequent organization, but this burden *decreases stepwise* in the course of development. The hindrance opposed to the modification of early stages of course is gradual, just slightly higher in a preceding stage compared to the respective subsequent stage. The *inertia* of these stages is a consequence of their *founding nature*!

These considerations substantiate the following sentence, which contains the dynamic explanation of the law of conservative preceding stages:

Insofar as (i.e. in those parts and properties in which) *the formative conditions of an ontogenetic stage produce physically* (i.e. continue in and thus partly condition) *those of the subsequent stage, the probability for a successful phylogenetic modification is always lower for the conditions of the early stage compared to those of the subsequent stage* under the circumstances of internal and external life conditions that can be assumed. The validity of this sentence is only made credible here by suggesting the essential causal connections; in order to give it greater stringency, very extensive and scarcely feasible investigations would be necessary. It would also need a wider formulation if our argument holds; indeed beyond the purely structural conditions other features of preliminary stages are of importance for the subsequent stages and are therefore prevented from phylogenetic modification. Our law does not seize these

37 other features; but we could view that as a special application of a more general law that would read: *Insofar as the conditions of a stage determine those of the subsequent stage in the effective context of ontogenesis, they must lag behind those later conditions in the course of phylogenetic modification of the ontogenetic pattern, in other*

words, they must be more conservative.—However, it cannot be the task of systematic morphology to test the validity of this more general sentence, not to investigate its extent of applicability, because it appears to belong to a general field of developmental dynamics.

For more detail see 1917, p. 29: “We imagine any morphogenesis to be made of a train of developmental actions, represented by orientated processes of growth, movement and secretion, each of which is triggered by a stimulus. Within closed morphogeneses this stimulus is a product of the germ itself and generally is given by the formative elements already produced”.

We thus have circumscribed a statistical law concerning the modification of ontogenesis in the course of phylogenesis, especially the modification of particular morphogeneses in the sense of the above definition (p. 8). I have formulated this law already in 1913 (p. 363) in a slightly differing version, and again in 1917 (p. 57) as the “*law of terminal modification*”. It reads: “*The stages of a morphogenesis (or terminal development in general) are so much more conservative in recapitulating the primitive development as they lie closer to the beginning, and so much more progressive as they lie closer to the end of the morphogenesis*”. The new formulation certainly expresses the same facts more clearly. I also consider the previously chosen *term* rather inappropriate, because we are not dealing here with a positive identification of actually occurring modifications, but with their prevention.

IX

The law of conservative preliminary stages can be considered to be the foundation of a *methodical interpretation of ontogenesis as a phylogenetic record*. In particular the phenomena of indirect development and of complex differentiation of simple rudiments provide an interesting material for such an application. We indeed consider formations arising directly, without considerable supplementary modifications, from their respective rudiments as relatively faithful recapitulation of corresponding ancestral stages (i.e. stages of those ancestors in which the rudiments first appeared in their present form and formative significance)—provided they are not of markedly neotenuous nature (p. 25). One has to beware of premature generalisations. Since we have

recognized how variably older and younger form states can be mixed in one and the same individual, indeed in the same stage, it is out of the question to consider the carrier of some primitive characters as primitive also with regard to other features without using appropriate criteria.

Wherever rudimentary states undergo a long series of modifications, be it *step-wise complications* or *simplifications*, or *modifications* of the primary *bauplan* and *rearrangement* of parts, we will surmise corresponding modifications in the series of ancestors. In this we cannot of course consider transitory stages of ontogenesis at the same level of significance as the adult formations, in other words we cannot interpret them as a direct *recapitulation* of “*finished*” ancestors and *ancestral organs* (p. 19). Paleontology indeed pleads against such an interpretation by bringing to light types which maintained certain correlations to the adult stage (by elaborating them in a more or less primitive manner), whereas these correlations are observed as transitory conditions only in extant organisms—paleontology indeed never shows truly embryonic or larval ancestors. A good example is the belemnoid insertion of the shell cone into the muscular mantle in juvenile stages of teuthoids and in fossil belemnoids, comparing Textfigure 28 with Textfigures 55 and 73!

There is indeed no point in talking about ontogenetic recapitulation of adult ancestral states. Strictly speaking, there is *no palingenesis* in the sense of F. Müller and E. Haeckel. Ontogenesis “recapitulates” itself in each subsequent generation, but with decreasing fidelity. If the term recapitulation is to be preserved, given its wide use, its meaning will have to be shifted to fit the facts—thus arriving almost by itself at what the authors actually had to say, and often really wanted to express. What is recapitulated are at best, namely in ascending development, the *bauplans* of ancestral stages (p. 4 and p. 35).

Conservative parts of individual development may then be called *palingenetic*, whereas *caenogenetic* would be used for processes that are modified from the type. This use of terms is acceptable only *in certain systematic contexts*; for ultimately any ontogenetic development has to be viewed as being modified, but modified at varying degrees.

Even a particular transitory stage cannot as a whole be identified with an ancestral stage. The instances of *heterochrony* indeed demonstrate that a given stage cannot be taken as being conservative as a whole, but rather that the components
39 (morphogeneses) have a certain degree of independence. Even in early embryonic

stages quite abnormal formations may appear, whereas the most general features are formed relatively late in development. But we *never* observe in a normal ontogenesis that a very special condition is transformed into a condition of general nature, i.e. that physically *the typical form arises from an atypical form*.

Among many other combinations, one may observe the case where the particular components reach at the same stage, i.e. simultaneously, a degree of differentiation already achieved in remote ancestors thus *composing a corresponding image*. Thus the human embryo at day 20 resembles a corresponding stage of the sting ray in a very astonishing fashion—something that does not occur before or after that stage in any comparable way. Such a coincidence may be secondary, however. In fact one finds much more closely related animals whose embryos are very dissimilar due to shifted correlations of components (Pls. 10 and 5), whereas the embryos of distantly related animals may look very similar (Pls. 4 and 17).

Certain *correlations* in developmental processes are conserved throughout large groups, whereas others are strikingly slack. It seems that certain parts always are correlated with certain others at certain stages, whereas each part is not regularly correlated directly with the whole, which at embryonic stages appears very plastic in timing and coordination of particular processes. This of course is a circumstantial observation concerning the relationship of largely comparable components with the whole that changes greatly in terms of their transient constellation. This phenomenon apparently reflects *no comprehensive law*, or else the requirement that the composition of rudiments at any stage has to insure viability and the capacity to generate subsequent viable and ultimately reproducible stages (preservability of all normal formations...).

According to our law, any systematic, phylogenetically orientated consideration has to scrutinize the particular reason (p. 22) for which preliminary stages are conservative in a given case. We may limit our scrutiny to the criteria allowing us to arrive at a visually seizable *form connection*, thus avoiding lengthy considerations on developmental mechanics. If we tried to base our decision about what is primitive and what is derived in ontogenesis on a more comprehensive formula (as given p. 37), we would indeed entangle systematic morphology in a net of difficulties for which it does not have the means to find a solution. However, we will gratefully accept what a dynamical morphology, i.e. the causal analysis of ontogenesis, has to offer in terms of well-established general knowledge. At present this is very little indeed. Based on my long
40 experience, however, one gets away with the following principle:

Insofar as, i.e. in those parts and properties in which, the formative conditions of an ontogenetic stage physically produce those of the subsequent stage, i.e. continue in them and thus determine them, they can also be considered phylogenetically more primitive than the latter ("Principle of phylogenetic reminiscences").

Practically and methodically this theorem affords everything the formula proposed by Haeckel was ever able to afford, but without its arbitrary and ambiguous features in conception and application. For here the relationships are spelled out clearly: 1. preliminary state and modification product in ontogenesis, 2. higher or lower age of the states in phylogenesis.—What is now needed is a *careful analysis* of the developmental process to permit recognition of its significance as a record in each special case. The developmental process should not be expected to provide information it is not able to give:

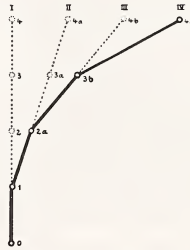
Above all, ontogenesis is *not* able to provide *any direct information* on the terminal states of *adult ancestors*, because it no longer contains such information. This observation is not always so absolutely negative in any given case. Indeed, since individual development always approaches definite formations stepwise, the distinction between transitional and terminal stages vanishes equally stepwise, so that *half-finished* organs can often give us a rather satisfactory image of the definitive (mature) ancestral state, from which they differ only little (p. 35). In return, evocation of that ancestral state becomes increasingly blurred in approaching the earliest rudiments that should lead us to increasingly early phylogenetic records. In general we will have to content ourselves with information on *primary, rough bauplan* and morphological *overall feature* that can indeed be obtained from such stages.

A conclusion from analogy may perhaps provide an idea about the actual product of a given rudimentary form in the ancestor. This is especially conceivable in species in which the same rudimentary form shows a direct (virtually rational) relationship to the functional organ (p. 19). However, a much more important insight stems from a systematic comparison of greater groups, in which a *terminal stage recognized as archetypal corresponds to a generalized rudimentary form*.

Here it must be recalled that we cannot reach beyond the relationships open to a purely systematic science of form (pp. 31 and 32), in other words: beyond the *representation of an ancestral series* as obtained from an interpretation of the genealogical pattern within the observed diversity of forms. This series thus *rests on the foundation* of pure systematics unless we are able to replace their principles and methods by

others that are based on a *comprehensive* knowledge of *laws of phylogenetic development*. For that the present considerations provide only a starting point, and a continuation cannot be expected in the near future.

A *direct determination* of the *real process* of historical genesis would indeed correspond more closely to a modern view of natural sciences than a merely conceptual order and comprehension of hypothetical relationships. They, however, are the immediately available base for observations and reflexion, whereas direct access to the past is *impossible*; a tidy system of concepts therefore teaches us more than pseudogenealogical hypotheses. One has to put up with that!



Textfigure 5.—General scheme of relations for the interpretation of a given morphogenesis in the sense of a phylogenetic document (Cf. Textfig. 2; from Naef, 1919, p. 60; see also Vol. 1, p. 34)

In the course of phylogeny, ontogeneses are recapitulated in an endless sequence. If the earliest stages of a given morphogenesis are most conservative, then they recapitulate rudimentary conditions of the most remote ancestral stages, while the subsequent morphogenetic stages recapitulate those of increasingly recent phylogenetic stages, up to the immediate ancestor. This relation is very insufficiently expressed by the formula "Ontogenesis recapitulates phylogenesis".

At any rate, development becomes increasingly indirect due to this relation: the earliest stages still "aim at" a very ancient terminal condition, while subsequent ones are orientated to increasingly more recent terminal conditions (which are more or less easily defined by the comparative approach). If, for example, IV represents the area of the *Sinus cervicalis* in a bird (the line 0-1-2a-3b-4c representing its development), then the dotted lines aim at the formation of the homologous zone in a lung-fish (I), in an amphibium (II), and in a reptile (III).

Finally, a *positive outlook* is nevertheless available: The last theorems (pp. 33 and 42) contain more than merely a translation of the preceding ones (pp. 24 and 25) in terms of special applicability. *Indeed ontogenesis recognized as a reliable record of phylogeny* sometimes provides more information than a group-genealogical interpretation of the system can provide. Thus ontogenesis grants a real extension of phylogenetic insight. For in many cases individual development passes through phases for which there are no adult representatives in the natural system, i.e. in the known extant

living world; thus it provides an indication about forms that would otherwise remain unknown to us. It thus gives us much more than a confirmation of what it has already provided as a foundation of systematic order (p. 14), namely a broadly based, *complete series of transitions* which relates remote *bauplans* with one another and places them in an undeniably *natural, real connection*.

Comparative embryology gains a special relation to systematics in that it often provides rather precise ideas for areas for which *the natural system shows wide gaps* (thus seemingly contradicting the old proposal according to which nature does not make leaps). For example, the transition from tetrabranchiates to dibranchiates is totally obscure in both systematic and paleontological terms. The embryology of cephalopods allows us to recognize stepwise how this gap is bridged by the organization of a developing embryo. Similar linkages based on embryology are possible in various other places, as will be shown later.

The "*law of conservative preliminary stages*" or the "*principle of phylogenetic reminiscences*" in ontogenesis indeed allow us to some extent to reach beyond the purely systematic consideration of organic diversity and to comprehend the process of *phylogenetic development directly* as it were, in its natural progress, at least in considerable, highly interesting sections.

Perhaps a more profound analysis will have to be envisaged, even though the suggested enlargement of morphological knowledge is still considered in the framework of systematic order: a higher concept of *morphological systematics* will ultimately cover the connection of types and *bauplans* as recognized in ontogenesis and place them in a wider ontological frame not only where they happen to be observed (i.e. in individual development), but also where they have their natural place in the context of ideas about phenomena in general, namely in a historico-morphological system. This will reach beyond the actuality of the observable "finished" or half-finished forms of animals and plants and try to define the ultimate order of past and present regularities in development. (Cf. e.g. Vol. 1, p. 791).

The individual development of organizations thus proves to be the richest and
 43 deepest source of systematic-morphological insight; it seizes the problem of unity in the diversity of phenomena and carries it from the realm of speculation in 'natural philosophy' to the domain of scientific research; it alone offers and promises a glimpse of the regularity of living development in general.

In the special sections we will find numerous opportunities to recognize the traces of the past in extant ontogeneses. In most cases it will be up to the reader to interpret them according to the above general, theoretical and methodological considerations. Only particularly important or easily misunderstood processes will be interpreted by us in an explicitly phylogenetic way.

II. MAIN SECTION

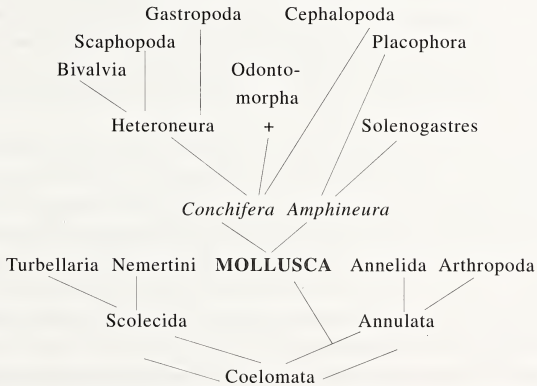
CHAPTER 1

On the Basic Concepts of Molluscan Morphology and Phylogeny

It is not possible to comprehend the actual processes, the description and figuration of which is the special task of this volume, without prior consideration of the greater context of organic diversity.

General morphological relationships of molluscs

(diagram of archetypal relations)



The above diagram expresses the purely *systematic relationships* among molluscan classes and of the phylum Mollusca to other Bilateria or Coelomata—independently of any phylogenetic supposition or inference. I have substantiated this diagram since 1911 in my “Studies on the general morphology of the Mollusca”, and no valid objections have been formulated. It is indeed of little importance if one or the other author studying this or that particular form considers the Mollusca as *descending* from the Turbellaria rather than from the Annelida, because we cannot seriously investigate that.

All we can show here is that typical similarity or systematic relationship of the circles considered here corresponds unequivocally to the above diagram. We refrain from the formation of a collective group within the *Coelomata*, although it seems likely that the sub-groups considered here are more closely related to one another (as “*Protostomia*”) and are opposed to another main stem, the “*Deuterostomia*” (plus the Tentaculata?).

The features arguing in favor of such a grouping within the Coelomata are not totally penetrating: The derivation of *mouth* and *anus* from the *blastopore* does not give much attention to whether the mouth or the anus, or both, or neither of them reveals their origin and genetic relationship, and the general derivation of the mesoblast from the primary endoderm, and the incremental growth of the entire coelomate germ from a *vegetational zone* in the anal area also weakens the contrast between formation of *mesoderm bands* and *gut diverticula* very substantially. The fact that this opposition is not applicable to the Tentaculata, in which both types of mesoderm formation occur, is further evidence for its doubtful systematic value. Nevertheless, it be too early to do away with it altogether (cf. 1924, p. 43!).

In contrast, the typical correspondence between *molluscs* and *annelids* should be emphasized. For it is linked to the earliest, undoubtedly *fundamental* processes of development and leads to the stage of a typical *trochophore*; although the latter may vary greatly, its primary overall features remain strikingly similar in both groups. This combination could therefore be expressed in a systematic category called “Eutrochaeta”; however, I think this group name would represent an unnecessary burden to a practical system, and I therefore will use it only for general considerations on the most comprehensive formative norms.

My ideas about the *archetypal* mode of development (*ontogenetic pattern*) of the Coelomata in general are summarized in Textfigure 6. Explanations can be given here

only in outline, with emphasis on those aspects that will be of special importance for the following descriptions:

1) The *vegetal pole of the egg* corresponds to the prospective ventral side, unless the latter undergoes secondary complications and shifts.

2) The *mouth* and the *anus* are formed (or at least positionally marked if they close transitorily) by the foremost and rearmost parts of the blastopore, the lateral parts of which become fused with one another.

3) The *animal pole of the egg* corresponds to the prospective apical disk, which is increasingly pushed forward by the budding growth of the anal zone, resulting in a bilateral structure derived from the original radial structure.

4) The *mesoblast* is formed by lateral, epithelial evagination of the primary endoderm, proceeding mainly from the anal budding zone, which in metameric forms gives rise to segments in a process similar to strobilation.

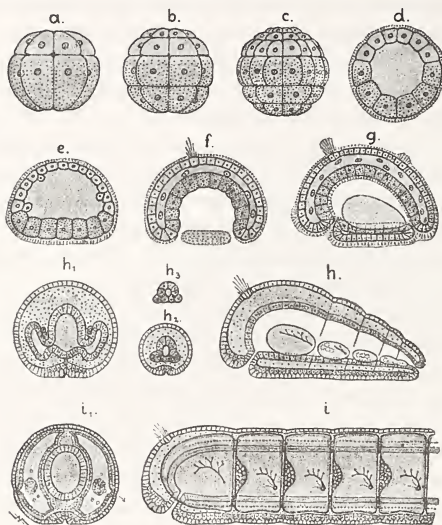
5) These *segments* can be viewed as incompletely separating individuals containing the basic capacities for all organ formations, especially for the formation of nephridia, gonads and coelomoducts, the latter (by losing their primary connexion with the gut and becoming connected to the nephridia) forming secondary issues of the coelomic sacs.

6) The ectoderm of the *blastopore lips* furnishes the central nervous system, which in coelomates thus originally forms a double, segmented strand lying on either side of the gutter-shaped blastopore seam, with an anterior and posterior loop surrounding the mouth and the anus, respectively. The mouth loop must be thought of as being connected with the apical disk. The resulting differentiations are widely variable (cf. p. 58).

7) The *primary mesenchyme* and its interstices from the system of blood vessels, the topography of which is determined by the epithelial organ anlagen (dorsal vessel, ventral vessel, segmental loops connecting them, gut sinus, tegumental sinus) the pulsatile parts receive the necessary space for their activity by protruding into the *coelome*, which is often conserved as a *pericardium* when all other parts have disappeared.

Textfigures 6h₁, h₂, h₃, show cross sections of the hindgut anlage of an ideal archetypal coelomate larva, from anterior to posterior. In the terminal part a single cell forms the connexion between mesoblast and gut, thus visualizing the conditions for a formation from few cells in a rudiment of this part of the body or in the entire bauplan

of such a stage: instead of *gut diverticula* a single *founder cell of mesoderm* can appear on either side, as is actually the case in the *eutrochaetes*.



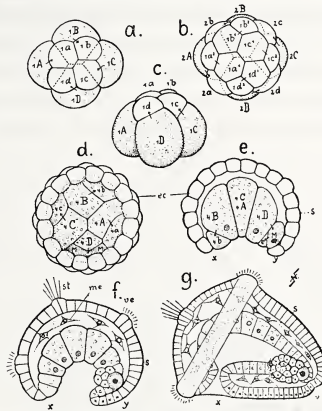
Textfigure 6. — Ontogenesis of an ideal archicoelomate in a schematic representation. It allows the ontogeneses of all bilaterians to be “derived” in the most straightforward and natural way, be it in the sense of a morphological gradation or in the phylogenetic sense of incessant mutation. We may indeed assume that the ancestor of all higher animals had roughly this form and development (p. 14). — All the stages of this development permit a phylogenetic interpretation as rudimentary conditions of a relatively primitive nature. Thus they suggest a protist-like stage a blastea stage, a gastraea stage, a shenula stage, and a helminthula stage in phylogeny.

For further explanations see Naef, 1926, pages 39-43 (*Biol. Zentralbl.*).

a-d: formation of the blastula, e: transition to the gastrula, with flattening of the ventral side, f: preparation for the formation of the mouth and the anus, and excentric shifting of the apical organ, g: bauplan of the stage corresponding to a trochophora, with coelomic pouches on either side of the gut; a cross section would be like in h_1 and could be easily derived from a simple gastrula. h_2 shows a cross section in the posterior part; h_3 hits only the outermost end of the coelomic rudiment and demonstrates the picture that would obtain if the bauplan of this stage had to be achieved by very few cells. — h visualizes the subsequent linear growth and the metameric subdivision, with the special participation of an anal budding zone. i and i_1 : differentiation of the anterior segments of the worm. The terminal stage is achieved by an extension of the coelomic pouches; each of them opens to the outside via the issues of the segmental nephridia, thus forming a short trunk; meanwhile the connection with the gut is interrupted. Between the gut and the coelomic sacs lie the main vessels, surrounded by the mesenchyme. On either side of the blastopore seam lies a ventral nerve cord with a ciliary gutter.

Compared to the Textfigure 6, the *molluscs* and the *annelids* present a *special case* of the general ontogenetic pattern; it is characterized by 1) spiral cleavage, 2) early stages made of few cells, *hence* formation of polar cells and mesoderm bands (Textfig. 7).

50 The idea that the blastopore opening narrows down by fusion of its lateral edges is the only conceivable one for interpretation of the various existing germ patterns, even where it cannot be observed directly. It is true that the *anus* does not remain
51 open, but undergoes a transitory closure, as is generally true with many other openings



Textfigure 7. — Archetypal stages of development in the Eutrochoeata, i.e. the natural-systematic group comprising the annelids and molluscs. (See also Naef, 1924, p. 33, and above Textfig. 6 a-g).

The upper sketches a-c show the typical spiral cleavage of molluscs and annelids. See especially Robert (1903) about *Trochus* from which these figures are copied. d-e represent gastrulation in a ventral view and in a sagittal section, f the early phase of blastopore closure starting posteriorly, the first mesoderm cells (M) marking the original hind end and prospective anus. (Small x are drawn instead of cell nuclei in the ectodermal cells of the seam); g is a trochophore stage with an anteriorly shifted apical field and beginning invagination of the stomodaeum, a nearly (except buccal zone) closed blastopore seam, growing mesoderm bands and an anal budding zone.

With special reference to molluscan development, note (1) the formation of micromeres by "spiral" cleavage from the macromeres; of the latter D marks the posterior, B the anterior end; (2) the formation of the first mesoderm cells (M, M₁) from 4d by symmetrical division at stage d, thus introducing the bilaterally symmetrical development for the subsequent stages. After the production of small hindgut cells (c) at stage e, these cells represent diverticula of the archenteron similar to those which generate the mesoblast of the Deuterostomia, but in an extremely reduced condition with very few cells. Their submersion in the blastocoel and their separation from the endoderm thus corresponds to an evagination.

(even well established ones) in higher animals—we will see other examples in the special section of this volume. This closure and later reopening generally occurs in a well-defined spot associated with the *mesoderm founder cells* or their direct descendants, i.e. the polar cells of the mesoderm bands, which mark the prospective *posterior end* of the *trochophore* once the blastopore has started narrowing down (Textfig. 7f, at y). In the meantime mesenchyme cells arise (ms) by submersion of primary ectoderm cells. The anterior end of the blastopore (x) becomes the mouth or pharyngeal opening.

- 52 While the question of *homology* between early developmental stages and their parts in *molluscs* and *annelids* is clearly answered by the facts, the problem of comparability of the adult stages is not easily resolved. Indeed the difference between a *Polygordius* and a normal mollusc (whatever the representative considered) is extremely large. The problematic Solenogastres have been called vermiform molluscs (Bütschli, Metschnikow), since their buccal-anal axis is considerably stretched and because they often show a particularly modest differentiation of parts; they have indeed been considered to descend directly from annelids or other “worms”. However, this is of little help for a strict comparison and comprehension of the types as long as we have no clear picture of the systematic-morphological relation of the vermiform and the other molluscs.

In a series of general studies (1911, 1913, 1924) I have therefore tried to build more solid foundations for these discussions by methodological investigations aiming at an outline of the archetypal developmental conditions, including advanced stages and the adult organization, common to all molluscan classes.

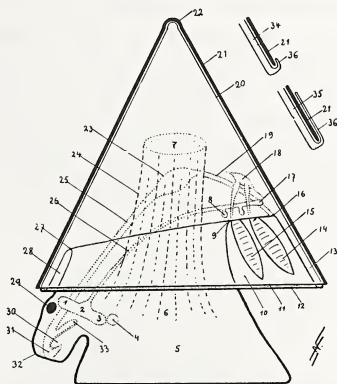
II

The diagram of Textfigure 8 should help in visualizing the issue (cf. Vol. 1, p. 51). It corresponds roughly to the usual, somewhat vague representations; it does not claim, however, that the stem species of the molluscs did look exactly or even approximately the same. Neither should it be taken to represent the inevitable norm or ideal image (archetype) for morphological deductions in all the existing organizations within the phylum; this sort of weighing can start at best from such a representation. The

distance separating it from an ideal, vermiform archecoelomate (or annelid) is so considerable that it is difficult to recognize homologies in even the most important parts.

As I have pointed out already in 1911, a *special comparison* of molluscs and annelids must relate to the processes through which they become differentiated starting from their common early stages. These are best represented in a diagram (Textfig. 9) to begin with; although it does not entirely correspond to any homologous stage of a special molluscan form, it comes so close to many of them that they can be easily projected morphologically or deduced by bauplan variation. But an ultimate truth should not be expected of this image; there is also no claim that the larval forms of all the molluscan stem species corresponded to this diagram.

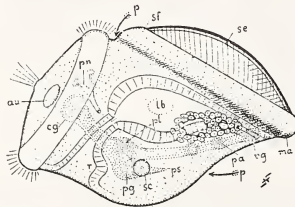
The reason why the morphological correctness of the two diagrams (Textfigs. 8 and 9) cannot be claimed safely is that a decision proved so far impossible about the primary or secondary nature of important elements of molluscan organization. In



Textfigure 8. – General scheme of molluscan organization (from Vol. 1, p. 51). 1: cerebral part, 2: pleural part, 3: pedal part of the perioesophageal nerve ring; 4: statocyst; 5: foot; 6: radiating muscles of the headfoot retractor or shell adductor; 7: insertion of the latter on the shell; 8: anterior branchial ganglion; 9: medial point on the anterior cross furrow of the mantle; 10: posterior part of the mantle cavity; 11: free shell rim; 12: free mantle rim; 13: mantle; 14: posterior gill; 15: anterior gill; 16: position of the anus in the middle part of the posterior cross furrow of the mantle; 17: visceral ganglion; 18: heart; 19: hindgut; 20: shell epithelium; 21: shell; 22: apex of the shell epithelium (embryonic shell); 23: midgut (stomach); 24: shell muscle; 25: foregut; 26: pleurovisceral strand; 27: anteriormost point in the mantle furrow; 28: anterior part of the mantle cavity; 29: eye; 30: tongue; 31: buccal cavity; 32: snout; 33: radula pouch; 34: section cut across the mantle rim with a weak shell fold (36); 35: section of a mantle rim with a more strongly developed shell fold.

particular the opposition between the two subphyla, Conchifera and Amphineura, is so thorough that we could consider either of them as representing an archetypal overall pattern, not finding absolutely valid criteria supporting a preference of one against the other. Since transitions are easily imaginable, one may use an intermediary diagram for an introduction, as we have done here. But the problem then is that the expected
 54 relation of the molluscan organization to the annelid organization is hardly deducible in morphological terms, and virtually impossible in phylogenetic terms. There is no point in trying to deduce the “archemollusc” of Textfigure 8 directly from a segmented “ancestral worm”; what can indeed be dealt with, as I have shown earlier, are the respective archetypes of the Conchifera (1911, 1913) and the Amphineura (1924). See also the corresponding view of Heider, 1914.

There is one congruence in the two subphyla in that likely *remnants of a* (probably annelid-like) *metamery* appear in very similar form in the most conservative types, namely *Lepidopleurus* and *Nautilus*. They appear in the only area where they could be expected according to the archetypal ontogenetic pattern, namely in the anal zone, i.e. in the typical *metameric budding zone* of the larvae and embryos of *all Bilateria*. In the diagram of Textfigure 9, I have therefore represented the anlage of mesodermic somites at this typical spot, which can be easily transposed into the corresponding zone of an adult mollusc (Textfig. 8). Given the typical annelid development, it would make no sense to look for a metameric organization in the anterior part of the body, which can be compared only with the larval head or acromerite (Hatschek).



Textfigure 9. — Schematic representation of a veliger stage following the trochophora stage, typical for the Conchifera, i.e. a more or less clearly planktonic, swimming larva with rudiments of the shell, the mantle (ma), the nervous system and sense organs, and with a concentration of the foot in the anterior part of the body; au: eye; cg: cerebral ganglion; pn: protonephridium; r: radula pouch; pg: pedal ganglion; pl: pleural ganglion; sc: statocyst; ps: pedal strand; lb: liver duct opening into the stomach; pa: pallial ganglion; vg: visceral ganglia; ma: mantle; se: shell epithelium; p...: approximate limit between the head-foot and the visceral sac, i.e. between anterior and vegetal regions of the conchiferan body. sf: shell fold, i.e. a delicate groove in which appositional growth of the primordial shell occurs.

These *remnants of metamerism* relate in particular to branchial sense organs, branchial vessels, cardial auricles, renal sacs, coelomic issues and parietal ganglia, and to connected, less common organs, and are grouped in a zone that arises from the 55 *anal area* of the larva, which becomes the *mantle cavity roof*. It must be stressed, however, that more than two metameres are complete, so that total suppression of metamerism and a corresponding bauplan simplification appear very near indeed (see detailed description of this phenomenon, 1913 and 1924).

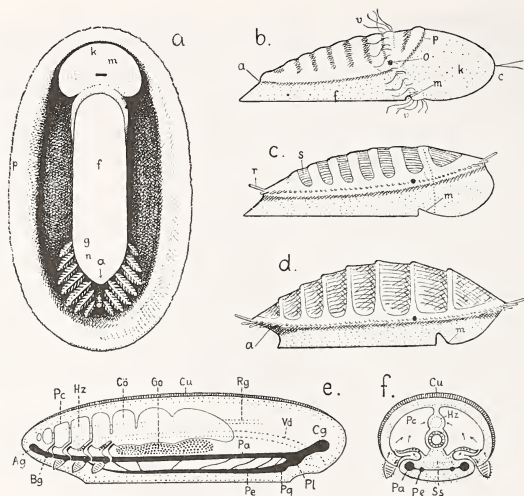
For a type *characterization* of the Amphineura we will use Textfigure 10. In (a) it shows a highly interesting advanced developmental stage of the most archaic extant placophoran form, which represents among the chitons what *Nautilus* is to cephalopods. It is remarkable that the juvenile stages of this form (more than the adult animals!), more than any other placophore or even solenogaster, resemble rather closely the Conchifera due to their archetypal molluscan features, from which some placophores and solenogastres have apparently departed more strongly. The following features should be emphasized in particular.

The posterior zone of the *mantle cavity* is strikingly *similar* to that of *Nautilus*, but it corresponds more closely to the archetype in one feature in which *Nautilus* departs from the primary condition (by pushing the anus forward).

In the archetype the *anus* lies indeed close to the *base* of the *mantle* (Textfig. 9!)—As in *Nautilus* and archaic gastropods, the terminal part of the body, namely the *roof* of the *mantle cavity*, projects posteriorly, the *gills* lying close to it on either side. The latter are already undergoing secondary multiplication, as indicated by the apparently incomplete anterior ones, but there are only 7 pairs, 2 of which are *associated* each with a *coelomic issue* situated anteriorly to their base, namely the renal opening (n) and the sexual pore (g). The posterior end of the strikingly weak foot is wedged in between, thus reducing the surface of the mantle cavity roof.

Only the early development, which unfortunately is unknown, could tell us whether the posterior pairs of gills belong to particular, incompletely differentiated metameres; however, it is possible that even these early stages would not provide the answer, to judge from my earlier experience with other chitons:

In chitons the anal zone with its interesting *metameric organ area* remains *strikingly long-inhibited* in its development, to attain its definitive arrangement only at a late stage by a very direct, probably abbreviated differentiation. A projecting mantle cavity roof, which could have allowed one to follow the progress of this differentiation,

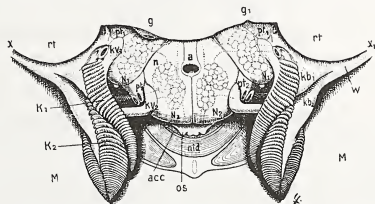


Textfigure 10. — Elements of placophoran morphology. a) a young *Lepidopleurus cajetanus* from the Posillipo (natural size 4.5 mm), seen from below. Compare with Textfigure 11 to see the general similarity in the arrangement of the pallial organs. The very low number of gills in this most archaic placophoran form and the concentration of the gills in the anal area are strikingly similar to the conditions observed in the anal complex of *Nautilus*. Much like in the latter, the nephridial (n) and genital (g) openings are metamericly associated with certain gill bases. a: anus; f: foot; p: mantle; m: mouth; k: head. — b-d are stages of *Callochiton doriae* (Capellini), again from the Posillipo. — b) Transition from the trochophore to the creeping juvenile stage, with temporary, subsequently definitive suppression of the swimming behavior. a: prospective position of the anus; v: velum; p: mantle bulge, reaching anterior to the velum in chitons; o: larval eye; c: paired frontal flagellum. — c) A young chitonid after loss of the velum, the former position of which is marked by the dotted line. m: position of the mouth; s: shell segment; r: marginal mantle spine. — d) A young chitonid with typical overall aspect, but still devoid of an open anus (a), of nephridia, coelom, heart and gonads, in other words with an undifferentiated mesoblast. — e) An imaginary transitional form between protoannelid and mollusc, as suggested by the anatomy and development of placophores, which is perfectly conceivable. It is indeed useful for a visualization of the overall morphology of molluscs and — given the ontogenetical evidence — of their relation to the corresponding annelid organization. The following traits should be especially noted: 1) The physiological and topographical connection between the lateroventral parietal strands (Pa) and the pedal strands (Pe), which grade anteriorly (Pg) into the ventral part of the perioesophageal ring; 2) The absence of a coelom in the anterior body part and the limitation of a distinctly metameric arrangement to the posterior part of the body; this may be due to a suppression of subdivision in the anterior part or to an excessive growth of the undivided cephalic part. — f) A cross section of e in the posterior region; the arrows indicate the course of the intersegmental loops from the ventral to the dorsal blood vessel; these loops carry the branchial vessels and segmental organs. The dorsum carries a flexible, thick cuticula (Cu). Ag: anal (visceral) ganglion; Bg: branchial (parietal) ganglion; Pg: pedal ganglion; Pl: pleural ganglion; Cg: cerebral ganglion; Vd: foregut; Re: dorsal vessel; Go: gonad; Co: gonad coelom; Hz: heart; Pc: pericardium.

is established only late in development by enlargement of a rudimentary zone which originally lies on the dorsum of the flatworm-shaped, creeping post-veliger stage (Text fig. 10 c, d). In modern chitons the projection of the *pedal sole* beyond the morphological posterior end clearly is a primary feature, thus allowing the sole to become the entire *ventral face* extending between the mouth and the anus.

III

The way in which molluscan organization appears related to annelid organization is certainly natural, as expressed in Text figure 10c. In ontogenetic terms, the imagined organism has to be based on the conditions of the younger stage given in Textfigure 7g, from which both molluscs and annelids are differentiated. This leads to the phylogenetic assumption, that in the ancestors of the molluscs fewer and fewer



Textfigure 11. — Dissected, slightly flattened mantle cavity roof of *Nautilus pompilius*, with attached gill and mantle parts (from Vol. 1, p. 70). Here we are looking at the surface of the metameric organ complex of an archaic cephalopod; it represents the retroflected rear end of the body. For its morphological interpretation, see Naef, 1913, pages 391-414, and in order to recognize precise homologies with an equally archaic placophore (*Lepidopleurus*), see Naef, 1924, pages 57-60, and above, Textfigure 10a. — The upper edge (section) of the preparation represents the anterior mantle furrow (x, x_1). The posterior mantle furrow lies below the gill insertion and the lettering (N_1, pt_2, kv_2, N_2 etc).

rt marks the insertion of the head-food retractors on the shell; g: genital pore; g_1 : opening of the pear-shaped vesicle; n: branchial nerve; a: anus; N_1, N_2 : anterior and posterior kidney sacs; pt_1 : field with the opening of the gonoduct; pt_2 : field with the opening of the metamericly corresponding pericardial funnel; kv_1 : root of the anterior gill vein; beside it lies the anterior kidney pore; kv_2 : root of the posterior gill vein; beside it lies the posterior kidney pore, laterally to the pore of the pericardial funnel; acc: outlets of the accessory glands; nid: field of the nidamental glands; os: posterior oosphradium; M: mantle; K_1, K_2 : anterior and posterior gills.

Probably embryonic stages of *Nautilus* and *Lepidopleurus* would show the relationships between metamericly arranged organs even more clearly than what a comparison of the adult forms of these archaic representatives of the two main groups of molluscs can do.

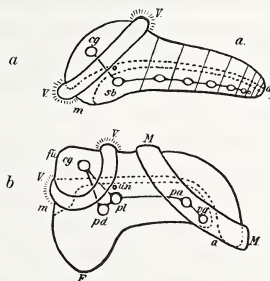
segments were formed while the dorsal surface of the creeping vermiform mollusc became covered with a thick, but still flexible *cuticula*. By secondary subdivision and consolidation this cuticula later would have become (as during ontogenesis) the octomeric *placophoran shell*.

Special difficulties arise in a comparison between this ventral face with its nervous centers and the corresponding parts of annelids. There are indeed two thick *pedal strands* passing through the placophoran foot and becoming united anteriorly to form a pharyngeal ring. But the metameric anal zone with its essential support organs is not linked to these apparent homologs of ventral strands, but to the parietal strands, which in the most archaic placophores are provided with segmental ganglia and are surrounding the anus in a way that must be considered archetypal for the central nervous system of all Bilateria. In the posterior part these parietal strands are completely separated from the pedal strands, because the latter do not reach to the end of the body, whereas anteriorly they are linked to the ventral part of the pharyngeal ring in a most characteristic fashion (1924, p. 59). The *homologs* of each of the two *ventral strands* thus are either the parietal strands alone, more likely the latter together with the ventral strands, the latter being considered as products of longitudinal splitting. This last view is supported by the special conditions of the Solenogastres (*Chaetoderma*) (cf. Lang, Mollusca, p. 202). However, given the situation known in molluscs, platodes, some annelids (Storch 1912) and chordates, one cannot exclude the idea of a *primary* "tetra-neury" of the ventral side in coelomates, with a relatively independent (more sensitive) lateral strand!

The *ventral surface* of annelids can thus be represented only partially in the *placophores* (cf. Text fig. 12), namely by the *anterior*, developmentally earlier part of the *pedal sole*, and—as to its posterior part—by the projecting mantle cavity roof. In ontogenetic terms this means: The trochophore or the veliger stage of chitons settles with its entire ventral side (Text fig. 10b), which corresponds only to the cephalic segment, and perhaps a few more anterior, still indistinct metamers, whereas the posteriormost segments are differentiated only later and then do not equally participate in the formation of the sole. A detailed analysis of these conditions is not possible here; Textfigure 10d shows at any rate that the belated growth of the morphological posterior end (a) and the parts lying immediately anterior to it do not contribute to pedal sole formation, even though the border line may be indistinct.

Textfigure 9 emphasizes the morphological *distinction* of *pedal sole* and primary

ventral surface, in that it approaches more closely the condition of typical Conchifera in which the foot is more markedly concentrated in the anterior body region at early stages already. Of course this could be a secondary condition, the mantle cavity roof becoming independent at an earlier stage in the Amphineura and thus being more conspicuous. Developmental stages of *Paludina vivipara* (Textfig. 16) and other gastropods indeed suggest that the foot is merely an appendix of the anteriormost body region or of the larval head, but this could just as well be the starting point of deployment as the final phase of limitation in a morphological series.



Textfigure 12. — Schematic representations for the comparison of mollusc and annelid organization (from Naef, 1913, p. 384). a) An annelid larva during differentiation of the segmented body from the anal cone forward. — b) A gastropod larva (*Paludina*) during the differentiation of the visceral sac from a corresponding rudiment (Textfig. 7). Compare the anterior body part of the annelid with the head-foot of the mollusc and identify the ventral surface of the mollusc. The latter is represented by the pedal process (F) in the anterior part, by the ventral side of the neck piece between the head and the visceral sac, and posteriorly by the prospective mantle cavity roof, which contains also the nervous centers of the posterior parts of the body. In the latter zone, we find the interesting conditions that allow us to use this figure for a topographical comparison with the annelid organization (cf. Naef, 1913, 1924). Compare the velum (V), apical field, cerebral ganglia (cg), protonephridial pore (un) and the nervous centers! The perioesophageal ring of annelids, with cerebral (cg) and subesophageal ganglia (sb), corresponds roughly to the molluscan ring. The pedal and pleural ganglia together represent the ventral part of the ring. The ventral strands of annelids are represented by the visceral connectives with their ganglia. pa: parietal ganglion; vg: visceral ganglion; fü: palp; m: mouth; a: anus; M: mantle (a slanting laterodorsal bulge in the posterior part of the body).

59 Quite similar conditions exist in the *mantle and shell*: In the Solenogastres a thick cuticula covers the entire dorsal surface (i.e. the greatest part of the body surface given the reduction of the sole). In chitons the early cuticula covers a large part of the dorsal surface of the larva (light zone in Textfig. 10b) and subsequently grows rapidly even larger, while the uncovered epidermis is relatively regressive (c, d). The

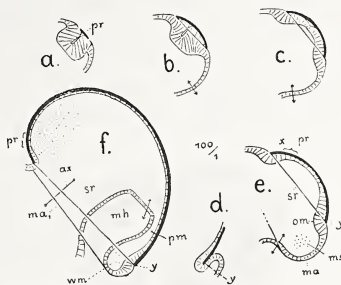
posterior part of the definitive shell that lies above the morphological caudal end, i.e. above the still-closed anus (a), appears inhibited, as indicated by the feeble development of the posterior shell segments that lie beneath the primary shell membrane, the hindmost of which is missing altogether at the earliest stage. Once the octomeric shell (d) is fully laid out, it occupies the entire upper surface, and the increasingly distinct mantle rim surrounds it entirely; not that the latter belongs to the cuticle-covered part of the body surface, even in the zone that later will be facing down and will reach inward to the limit of the mantle cavity (Textfig. 10a). This whole part is comparable to the shell surface and the underlying epithelium to the shell epithelium of the
 60 Conchifera, but it is *by no means* entirely *homologous*: Indeed the soft mantle rim of the Conchifera is not covered by a cuticula, instead it is ciliated and does not include the upper surface of the larval head, being limited to the post-velar part of the veliger.—Is this state primary or secondary?

This restriction is all the more valid for *shell membrane* of the Conchifera, which covers only part of the upper surface of the larval body, even after its extension and overall approximation of the early placophoran shell form (Textfigs. 10 e and 13 e). This part bends inwards in a most characteristic fashion at even earlier stages (Textfig. 13 a) to form the “*shell gland*”, so that the marginal cells virtually meet in one point where they start to form the first, extremely small *primordial shell*. With the *marginal growth* of this first shell, the *shell epithelium* rapidly flattens out again to establish the definitive relationships with the shell. If we call the structure thus obtained a *cuticular* one and compare it roughly with the placophoran shell, it becomes quite clear that we are faced with a very peculiar product, at any rate that only the *matrix* of the *shell rim* is corresponding to it. The considerably larger, central part of the shell epithelium should rather be called a *glandular epithelium* which *continues* to build on an existing cuticular structure.

This means that either the differentiation of the shell epithelium has been suppressed in the Amphineura, or it has been added as a new element in the Conchifera. Certainly, the latter appears more likely; but a detailed consideration of the process shown in Textfigure 13 leaves us with some doubts; for it is undeniable that the typical rudiment of the shell gland appears *extremely early* in the Conchifera, indeed often simultaneously with gastrulation (cf. e.g. Meisenheimer 1901).

One will therefore be tempted to consider it a *very ancient* organ of enigmatic phylogenetic significance (cf. 1924, p. 61). It must at least point at a past phase of

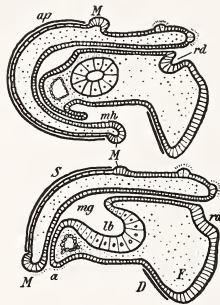
phylogeny *prior* to the special formation of the conchiferan shell. Textfigure 13 b provides a basis for understanding this formation if we consider the following point: The ectodermal invagination is not the organ directly producing the shell but a differentiation inside that organ, the *central part of shell epithelium* being excluded from participation in the archetypal formation of a cuticle that is made entirely by the marginal cells of the "shell gland". Thus below the primary shell produced lies a true gland, the secretions of which reinforce the inner shell side. The mode of cellular participation in shell growth changes (or merely starts) when this gland flattens out; there is little doubt that Textfigure 13 b represents a phylogenetically older state than d, e and f.



Textfigure 13. — Development of the shell and mantle epithelium in typical conchifers. The parts are represented transparent, so that the shell and mantle epithelium, and the shell itself, can be drawn as in a medial section. a, b, c, d, e, f show stages of *Lithoglyphus naticoides*, slightly simplified from whole mount preparations (1/100 natural size). (Compare the conditions of Textfigs. 7 and 9 with corresponding modifications). In typical conchiferans the shell rudiment is localized by the formation of a shell gland (a) from an invagination of the shell epithelium. Subsequent flattening (b, c) integrates the lips of the invagination into the matrix of the ostracum (om), the deep part of the "gland" into the matrix of the hypostracum. The former maintains a solid connection with the edge (x, y) of the primordial shell, whereas the latter is only loosely apposed. Thus from the beginning the shell epithelium shows a differentiated relation to the shell itself, beyond which reaches the "soft" rim of the mantle (mm, ma). Below it the mantle cavity (mh) forms by a progressive invagination around the anal zone, combined with the broadening of the mantle rim (the double arrow marks the position of the anus, which will open very late). pr: truly primordial shell without growth lines; it is apparently produced by the ostracal matrix prior to its full differentiation (rather than by the deeper part of the invagination). — Since this is a gastropod, the shell will soon show excentric growth (spiral winding). In the course of the process figured, the anlage is in fact rotated around the axis marked ax, by about 180° (torsion); this movement is omitted here. — d) Formation of a deep shell groove in *Paludina vivipara*, by an extension of weak shell fold over the rim of the ostracum. This permits secondary additions (periostracum) produced by a "secondary shell epithelium" facing the outside of the ostracum; in this case they form a protective membrane with longitudinal rows of bristle-like spines at later juvenile stages. In the rather closely related *Lithoglyphus*, no such formation exists, although a shell groove is still recognizable, as seems to be the case in many (perhaps all) conchiferan molluscs, at least as a transient formation.

IV

The formation of the shell is linked to the formation of the enclosed body part, which we call the *visceral sac*. The latter is limited at its surface by the shell and mantle rim; inside a natural distinction between the visceral mass and the *cephalopodium* is increasingly difficult with increasing (dorsoventral) flattening of the whole animal. It is virtually impossible therefore in the Amphineura, independently from the question whether this is a primary or a secondary state. The latter is at least equally well conceivable since many gastropods demonstrate through their postembryonic development how a 'segmented' structure can be transformed into a totally flattened mollusc (cf. 1911). In the embryo, however, there is a (much earlier) process that is inverse, however: From a *flat* visceral sac a *highly vaulted* one is made (Textfig. 17) which finally may become deeply conical; the question could thus be considered settled.



Textfigure 14. — Sketches explaining the formation of typical conchiferan veliger stages: 2 advanced stages of *Paludina vivipara* in medial sagittal sections (about 1/100 natural size; from Naef, 1913, p. 383, Fig. 6). Torsion is not shown, the operculum (D) is added too early (in fact only the opercular gland is recognizable as an epithelial thickening at that stage). The liver (lb) is in asymmetric communication with the stomach (mg), the right side rudiment having degenerated. — Note the shape of the mantle sac (posterior body part) due to the retroflexion of the anus (a) and mantle rim (M) and the formation of the mantle cavity (mh) by invagination and folding over of the mantle. The shell (S) grows by strongly excentric apposition of material added to the rim by the ostracal matrix (cf. Textfig. 8). The ventral side is subdivided into a gutter sinus, a creeping sole, an opercular gland, a neck piece, inner wall, roof and outer wall of the mantle cavity. The primary position of the anus lies between the latter two parts. Note the typical subdivision into a head-foot and a mantle sac. rd: radula pouch; ap: shell apex; f: foot.

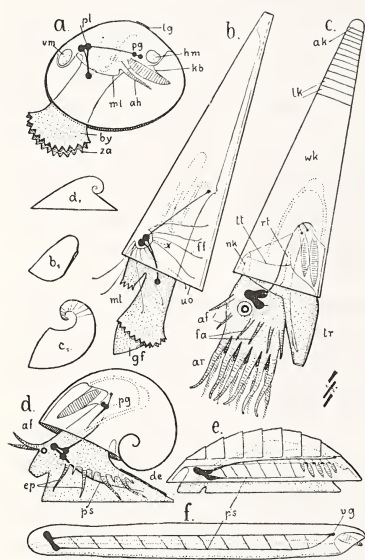
63 However, one should recall that the molluscan form is established only by the *retroflexion* of the gut, the roof-like mantle folding producing a *mantle cavity*, and the establishment of a shell and foot; viewed phylogenetically, these processes could represent a part of premolluscan or of early *molluscan* history. If we consider the likely vermiform ancestors, these processes may change in aspect. They would then be reminiscent of those observed in semisessile worms which live in tubes (chaetopods, gephyreans, tentaculates), making the molluscan shell a peculiarly perfected *living tube* (cf. Heider 1914, pp. 506-507, Naef 1924, p. 104). This possibility is mentioned here only to show that in spite of the above observation the archetypal molluscan organization can be seen closer to the Conchifera, in which the basic shell form is more or less deeply conical whereas the early rudiment is rather flat, bowl-shaped.

This again leads to considerations about the primary 'segmentation' of the body: in Conchifera the *differentiation* of a *cephalopodium* and a *visceral sac* is a *fundamental* phenomenon that is of the greatest morphological and physiological significance (cf. 1911, pp. 83 and 99). It separates the *animal* body section from the *vegetative* one in a surprising decisiveness and leaves for the intermediate section only the following general (archetypal) connecting parts: cephalopodial retractors (shell muscles), oesophagus, parietal strands, cephalopodial artery, sinus-shaped cephalopodial vein. Within the Conchifera any obliteration of this 'segmentation' is easily recognizable as a morphologically secondary state. What are the conditions in the Amphineura?

Have the Amphineura formed an increasingly broad connection between the foot and the shell, with a *patelloid obliteration* of the 'segmentation' under discussion (p. 62)? Or has that 'segmentation' become established through an increasing elevation of an originally flat cone, having led secondarily to a corresponding autonomy of the parts and better mobility in the ancestors of the Conchifera?

Archetypal Conchifera have a *narrow shell opening* permitting projection of a more or less *structured cephalopodium*, in which generally the head and the foot are not really distinct (1911, p. 85). Even in the degenerate scaphopods and bivalves—which probably form a homogeneous type or phylum—the foot is much more clearly structured superficially than in any amphineuran, and wherever the foot forms a *simple creeping sole* in a conchiferan, this condition is undoubtedly a systematic-morphologically *derived* condition. But could this be true also in Amphineura, or should we surmise an initial ascent from a simple to a complex locomotor apparatus in the archetypal Conchifera or their preliminary stages?

64 These questions and ensuing ones do not yet permit a comprehensive consideration and description of molluscan morphology, as I have shown in 1924. This particularly prevents a concise presentation in teaching, because any "if" and "but" is of little use there, although a *definitive formulation* of the *basic concept* (Textfig. 8) may on the other hand appear like a violation of the facts. Hopefully these difficulties will be overcome with the present volume through unequivocal elucidation of the main types. We have to rely especially on the comparison of the particularly advanced, most *differentiated* forms whose complex ontogeneses provide the best information on preliminary stages in phylogeny and archetypal bauplans. Such forms are, as in the presentation of 1911, the Gastropoda and the Cephalopoda.



Textfigure 15. — Schematic representation of the original types of the 6 extant classes of Molluscs (from Naef, 1924, p. 47). — a) Bivalve. — b) Scaphopod. — c) Cephalopod. — d) Gastropod. — e) Placophor. — f) Solenogaster. d₁) Diagram illustrating the (always secondary) flattening of the shell in gastropods. — b₁) Diagram illustrating the secondary formation of a terminal hole derived from the primary shell opening in scaphopods, and of the shell division in bivalves. — c₁) Diagram illustrating the derivation of spirally coiled shells from straight ones in cephalopods.

Of the inner organs, only the general arrangement of alimentary canal and the topography of the central nervous system and sense organs are figured. Homologous parts can easily be identified; cf. Textfigure 8 add vm: anterior shell adductor; pg: branchial and pallial ganglion; lg: ligament; hm: posterior shell adductor; kb: branchial band; ah: appendage of the buccal lappets (ml); by: byssus gland; za: marginal peaks of the split anchoring foot; oö: upper opening of the mantle cavity and shell (in b: not labeled); ff: prehensile filaments; x: cephalic lobe; uö: lower (normal) opening of the mantle cavity and shell; mt: buccal tentacles; gf: medial wedge-shaped part of the anchoring foot; af: ocular palp; fa: palp arms; ar: prehensile arms; tr: funnel tube; nk: nuchal attachment; tt: funnel pouch; rt: funnel retractor; wk: living chamber; lk: air chamber; ak: initial chamber of the shell; pg: pallial ganglion; in Fig. d with separate branchial ganglion; ep: epipodial palps; ps: pedal (nerve) strand; de: operculum.

These figures are the result of a careful abstraction, based on personal investigations into the structure and development of living and fossil molluscs; they should not be confused with the diagrams in many current text-books. However, one might note that in a), an outline of *Solenomya* (i.e. a form stretched in the longitudinal axis, with a nearly straight dorsal line) could have been used instead of *Nucula*. In b), the wedge-shaped process (gf) of the digging foot of *Dentalium* could be omitted, so that the similarity with Figure a) would be enhanced. In c), the shell shape could be figured blunter (cf. Textfig. 17 a₁).

V

To be able to consider cephalopods in comparison to gastropods, one has to comprehend the process of *torsion*, which I have therefore tried to interpret and disentangle first from confusing accessories (1911). This implies knowledge of the archetypal *body architecture* of the conchiferans, as shown in Textfigure 17b (cf. top of p. 68), and of the evolution of *spiral coiling* of the shell, the establishment of which is shown in Textfigures 13 and 17e. The latter phenomenon is likely to be a partial cause for the phylogenetic occurrence of torsion, as shown in 1911, whereas the subdivision into a cephalopodium and a visceral sac, which are united by a rather slender, flexible connexion, made torsion mechanically possible. In archetypal gastropod forms (1911, p. 159), i.e. in Zygobranchia and—only slightly less distinct—in Trochomorpha and Docoglossa, torsion is brought about by a 180° rotation of the visceral sac against the cephalopodium, similar to the position of the head in a sleeping bird.

During torsion the *primary symmetry* of the inner organization, as far as it is already established, remains relatively undisturbed in both the cephalopodium and the visceral sac (*Scissurella* and *Fissurella*); the shell apex changes from an anterior exogastric, via a sinistral, to a posterior endogastric position, whereas the mantle cavity moves via the right side anteriorly. Really *twisted* (in a true "torsion") is **only** the middle piece in which the parietal strands thus cross over each other (Textfig. 17e, f).

This "only" is not meant to imply a mathematical precision. The *shell muscles* in particular undergo a more or less asymmetrical formation during torsion, and this asymmetry is later handed down mechanically to the connected parts as far as they have not yet undergone the corresponding change. The shell muscles appear to be programmed for torsion already in their rudiments; thus the muscle originally inserted at the right side of the shell either moves over to the left side (*Fissurella*) or degenerates altogether. In all the gastropods torsion therefore results in a *tendency* to develop various parts *asymmetrically*.

This tendency concerns the *shell* (which projects to the left side) and the inner organs, which follow the shell stepwise in younger gastropod groups. The resulting modifications of the archetype (cf. 1911) appear, more or less prematurely, in the otherwise conservative juvenile and embryonic stages, in which the *primary symmetry* of the trochophora stage is *sooner or later lost*, the normal body 'segmentation'

becoming partially obliterated or retarded. In the Monotocardia the process of torsion therefore tends to lose its typical aspect and becomes amalgamated with secondary modifications of organization.

A comparative presentation cannot be given here; but I would like to give here at least a few special remarks on the process as it occurs in *Paludina*, which I had presented very simplified in 1911 (Textfig. 16): In this gastropod, which differs from its relatives by the lack of yolk, the archetypal picture of the rotation is more easily recognizable than in other Monotocardia. It essentially occurs at stages at which the general conchiferan *body structure* is already achieved so that the rotated medial part becomes very distinct.



Textfigure 16. — Four veliger stages of *Paludina vivipara* showing the typical process of torsion (from Naef, 1911, p. 102). About $80\times$ natural size. — a) An almost straight form that could be easily compared with the original conditions of the earliest mollusc (cf. Textfig. 8). If torsion is omitted (an abnormal phenomenon observed occasionally), development indeed proceeds in that direction for some time. Note the thick, soft mantle rim which is much wider than the shell; it corresponds to the muscular mantle of dibranchiate cephalopods. — b) The mantle cavity formed by the growth of the mantle and by invagination turns to the right side, while the apex (ap) or initial shell begins to rotate to the left.

c) This rotation is advancing so that the mantle cavity comes to lie more anteriorly, the shell apex more posteriorly. The further process of finishing torsion is not simply pushing it to 180° , since complicated rearrangements occur in the visceral complex that move the completely asymmetric mantle cavity to its anterior position. Stage d) is in fact has a visceral mass not yet fully rotated, and it would not be as symmetrical as suggested by the figure. The operculum (D) in fact is not yet formed at that stage.

It is true that the rotation starts slightly earlier than stage a and goes somewhat beyond stage d (Textfig. 16; cf. 1911). A *typical torsion through exactly 180° does not occur; neither in this form nor in any other monotocardian*, in fact it is not conceivable since the increasingly asymmetric development during torsion would not permit an identification of the end point. For example, the anus never reaches a truly anterior position, because the right (originally left) side degenerates too soon. In an attempt to emphasize the typical process, I had not paid too much attention to the special case of *Paludina* (which I had studied several years earlier) and in writing the text followed my slightly diagrammatic figures. This specification is in no contradiction with the

67 general understanding of the process of torsion, and the somewhat short-sighted adverse criticism by Andersen (1925, *Morphol. Jahrb.*, pp. 192-194) does not need to be discussed here; comparative abstraction and painstaking description are indeed two different matters. Andersen seems not very interested in the former, and the latter was not intended by me in the publication mentioned. My Figure 16d represents a stage in which torsion is forcibly pushed to completion as it were (as may happen in preparations), the shell having about one-half convolution. (The very moment of completion of a convolution also cannot be determined more precisely!).

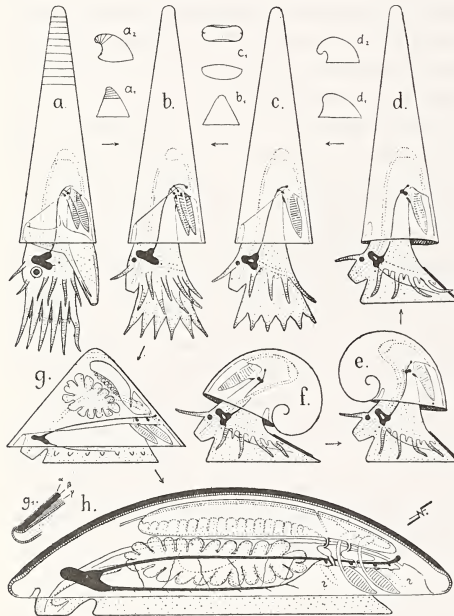
A correct comprehension of torsion in gastropods enables one to compare their organization in every detail with the conditions of other molluscs, beginning with their closest systematic relatives, the bivalves and scaphopods with which I have united them as *Heteroneura* (1924, p. 88). The primitive form of this group (Textfig. 17c) can be imagined as a mollusc with a more or less markedly high, conical shell, a single pair of gills and a structured cephalopodium that is intermediary between that of the most archaic gastropods (*Scissurella*) and that of the lamellibranchiates (*Nucula*), at any rate way above the diagram given on p. 53. Indeed a greater simplification of the foot is not conceivable for the form considered since we have to compare the archetype of cephalopods (Textfig. 17a) with this hypothetical form—according to the systematic relations explained on p. 47—rather than with a purely imaginary primitive mollusc.

Similar considerations lead us to an *archetype* of the *Conchifera* as shown in Textfigure 17 b, i.e. a molluscan form of similar overall aspect but with at least 2 pairs of gills and associated parts in the mantle cavity roof. Again, a greater simplification is not conceivable since we have seen at least dimeric differentiation of this part in the *Amphineura* as in the *Cephalopoda* (1922, 1924, p. 59).

VI

Thus *two strongly opposite basic or archetypal molluscan forms* are facing each other (Textfig. 17 b and h), each of which suggests a different phylogenetic derivation. As I explained in 1924, we had no valid reasons at that time to choose and thus had to remain with an *undecided alternative*. But we can imagine an intermediate form and in fact have to suppose it for phylogeny. I have already given it (Fig. 8) as

an introductory diagram, and I repeat it, slightly modified, in Textfigure 17 g (cf. also 68 Textfig. 25a). This intermediate form will now be given a muscular foot with (not yet fully defined) epipodial senso-motor structures and a *Patella*-like shell as known since the Cambrium in various modifications from forms of unknown systematic position (cf.



Textfigure 17. — Diagrams for a comparison of the main types of molluscs, and as a basis of discussion about a general ancestral form.

a) Ancestral form of the cephalopods (*Orthoceras*-like, Cf. Textfig. 21. — f) Ancestral form of the gastropods (*Bellerophon*-like). — h) Ancestral form of the amphineurane (*Lepidopleurus*-like). — e) A pure construction showing a gastropod with revoked or omitted torsion, a bauplan that is only occasionally observable in malformed gastropod embryos or larvae. — d) A gastropod construction based on omission of both torsion and volution, facilitating comparisons with other molluscs. — c) Ideal ancestral type of the heteroneurans, valid also for the fossil Odontomorpha. — b) Ancestral type of the Conchifera. — g) A transitional form constructed to relate b) and h) with one another. The question is in fact whether we can imagine the ancestral molluscan type according to the outline of b) or that of h); only the organizational conditions represented by h) are obligatory, as expressed also by Textfigure 8, which is approaching the conchiferan condition. The shell then has to be

imagined as a flexible cuticular mass.

Accompanying figures: g₁ illustrates the typical mode of appositional shell growth in the Conchifera. The marginally growing ostracum (β , black) increases in thickness distally as function of body size increase, the internally added hypostracum (γ) increases in thickness apically; α marks the cuticula, which is possibly archetypal as well; it is added in a delicate gutter of the mantle rim (shell groove). If it is specially enhanced by a covering fold, the cuticula becomes a "periostacum", such as the additional main shell layer of dibranchiate cephalopods.

a₁ and a₂ are archaic cephalopod shell forms, b₁, d₁ and d₂ are patelloid variants of types b) (c) and d), without any further identification, like those encountered in early paleozoic strata. c illustrates a transformation of the shell that might have led to the bivalve condition (from c, via b₁, to c₁).

The arrows represent the direction of morphological "reduction"; the representations of the (theoretically conceivable) transformations of course go in the opposite direction. A didactic treatment of the phylum would best start out from Figure g.

69 1924, pp. 50-51). For such forms are imaginable in primitive molluscs or primitive conchifers (Odontomorpha) alike, or in almost any gastropod group and also (with the characteristic chamber formation) in cephalopods. It is unknown, however, whether the major groups of extant molluscs really evolved from a situation like Textfigure 17 b via g to h, or in the inverse order, and whether we should indeed start from either one or the other form rather than from an intermediate one in our systematics.

We can raise the *question* here already *what sort of evidence* we need to *come to a conclusion in the problem formulated* above. This evidence can only be obtained from ontogenetic data provided by an indirect development (p. 42). It seems inconceivable that one of the given types reveals itself directly as truly primary; so we have to find which one is of *clearly derived nature* in at least one of the essential characters. If e.g., *Lepidopleurus* turned out to first differentiate its foot only in the anterior part, the anlage subsequently only becoming enlarged posteriorly, this would mean that the placophoran type suggests an archetype corresponding to Textfigure 17 g. Inversely, the above situation would have to be considered *secondary if in a conchiferan the foot anlage originally reaches to the anus and only subsequently becomes reduced to finally become associated with the mouth area as is typical in this large group*; thus an archetype like in Textfigure 17 g would obtain, from which that of Textfigure 17 b would have been derived secondarily. The third chapter will show that this is indeed what happened.

In the first part of my molluscan studies (1911) I had reasons to reject the premature, indeed unmethodical view according to which the Conchifera or Eumollusca are derived from Amphineura (loc. cit., p. 76) and to propose an inverse relationship (p. 77). Here I again approach the usual view. This should not be taken to mean, however, that I use the method of naive phylogenetics and arrange Vermes, Solenogastres, Placophora, Gastropoda and Cephalopoda in a single series, each group having its ancestor in the preceding one. What I really mean is that a methodical comprehension of the respective types of classes, superclasses and subphyla makes us realize that the amphineuran type shows a primary nature in important *features of overall aspect*. This is true also for many other features but does not exclude the possibility that the conchiferan type shows primitive characters no longer present in the Amphineura.

70 Only comparison of both types can provide scientifically sound ideas about a common ancestral form.

CHAPTER 2

On the Particular Initial Conditions and Aims of Cephalopodan Ontogeneses

Contents: I. General morphology of cephalopod egg. II. The general primitive form of cephalopods as the primary final aim (p. 75). III. On the development of *Nautilus* and on the contrast between it and the dibranchiates (p. 79). IV. The particular primitive form of the dibranchiates as the secondary final aim (p. 85).

I

The particular properties of the embryonic development are due to a peculiar constitution of the egg. This is visible in cephalopods even from rather superficial observation. Their eggs are always of unusually large size, which is exceeded only in vertebrates; it never falls below a certain minimal size. The egg of *Nautilus* is among the largest, indicating that there is no secondary egg size increase within the class, but that extreme yolkiness of the egg is an archetypal feature. As far as is known, the smallest eggs are those of the genus *Argonauta*; comparative considerations lead to the conclusion that this genus reaches, in this as in other features, an extreme situation within a particular evolutionary tendency. The eggs of *A. argo* have a length of less than 1 mm. The largest eggs I observed were those of large sepoids, such as *Sepia officinalis* (large variety), *S. orbignyana*, *Rossia macrosoma*, in which the egg length reaches 7 mm. But *Nautilus* does not fall short of these; the largest ovarian eggs in a semi-mature specimen of *N. pompilius* were

about 6 mm in length. (Precise indications are not possible given the state of preservation of this material)*. In the large-egg octopods (cf. Vol. 1, p. 692) the length of the egg is similar to or higher than these measurements. (cf. below on *Eledone*).

The following list shows that the egg size of most forms varies between 1 and 3 mm; I consider the higher value the more representative of the archetypal condition, since the species producing small eggs, at least among decapods (oegopsids) are clearly atypical as indicated by their modified embryonic development.

- 71 Egg sizes : *Nautilus pompilius* 5 × 7**, *Loligo vulgaris* 1.6 × 2.2, *Loligo forbesi* 2.4 × 3.3, *Alloteuthis media* 1.1 × 1.5, *Alloteuthis subulata* 1 × 1.3, *Abralia veranyi* 0.8 × 1.0, *Illex coindetii* 0.9 × 1.1, ommastrephid y 0.8 × 1, oegopsid x** 1.2 × 1.5, *Sepia officinalis* 4.6 × 6-7, *Sepia orbignyana* 4.5 × 7.2, *Sepia elegans* 3 × 4, *Rossia macrosoma* 5.3 × 7, *Heteroteuthis dispar* 1.8 × 2, *Sepiolo robusta* 3.6 × 4, *Sepiolo ligulata* 2.2 × 2.6, *Sepietta oweniana* 2 × 2.4, *Sepietta obscura* 1.9 × 2.2, *Rondeletiola minor* 1.3 × 1.5, *Octopus vulgaris* 1 × 1.8-2, *Octopus saluzzii* 1 × 1.8-2, *Octopus macropus* 1 × 1.8-2, *Octopus defilippii* 0.9 × 1.6, *Eledone cirrosa* 3.5 × 6, *Eledone moschata* 4.3 × 13, *Scaevurgus uniccirrus* 1 × 2, *Scaevurgus tetracirrus* 1 × 2, *Tremoctopus violaceus* 0.9 × 1.5, *Ocythoe tuberculata* 0.9 × 2, *Argonauta argo* 0.6 × 0.8.

(These measurements cannot be given with absolute precision. They vary strongly even within species, and they can only be taken on fresh material measured under water. Egg capsules are not included in the measurements.)

Egg size is not proportional to body size, not even within smaller groups, e.g. sepiolids or octopods. It is related to special adaptations, some species producing a small number of well-developed young hatched from large eggs, whereas other species produce large numbers of larvae-like (pelagic) juvenile forms that develop from small eggs. This clearly distinguishes e.g. *Eledone* and *Octopus*, the former having large, the latter small eggs; in *Eledone* a finished animal hatches from the egg, whereas in *Octopus* the hatchling is a true larva (Plate 30). In octopods as in decapods nektonic

* Scientific Editor: It is not clear why Naef does not mention the indications by Willey (1902, p. 809): "I have recorded instances of nearly mature females...the largest ovarian ova...attaining a length of 17.6 mm and a maximum breadth of 15 mm".

**Scientific Editor: The text says "oegopsid y"; this must be an error since the plates show only an "oegopsid x". Furthermore, in some octopod species, the egg sizes given by Naef do not correspond to more recent observations.

forms show a tendency to reduce egg size whereas the benthonic forms tend to increase egg size.

Oogenesis has been studied by earlier authors (Kölliker, Lankester, Ussow, Vialleton...) who provided indications on the mechanism responsible for the production of such large eggs (cf. Korschelt and Heider 1909, p. 320). A description of these processes is not necessary here. On the other hand, I have to emphasize that in contrast to the description by Faussek (1896) the gametogenic zones, and in particular the oogonia, cannot in general be distinguished from the mesendoderm at very early embryonic stages already, and neither can they be derived from the ectoderm as indicated by

Teichmann (1903). The gamete cells do not arise from the coelothelium, as indicated by Bergmann (1902, 1903), but from a cell group that becomes distinct by stage X-XI (Fig. 1-3, Plate 4), at a time when the rudiments of the heart and pericardium become distinct. It arises from the mesendoderm and in female individuals it reveals the faintly staining oogonia very distinctly (cf. Naef 1913).

The spawned eggs are surrounded, at least in the decapods, by gelatinous envelopes, which contain several eggs (minimum: 4) in the teuthoids, one egg in sepioids; similarly in *Nautilus* (Willey 1897). The structured egg masses thus formed can be glued together secondarily to form larger spawns. When leaving the ovary, each egg already has its own, chitin-like, tough, thin, transparent envelope, the so-called "chorion". It encloses the ovum very tightly in decapods, less so in octopods; in the latter it is drawn out into a long, hollow stalk at one end, whereas the opposite end contains the micropyle.—Within the chorion the ovum is generally situated so that the formative yolk lies close to the micropyle (especially in octopods); occasionally an inverse position occurs, which results in a fatal situation when the hatchlings are unable to leave the chorion (cf. Vol. 1, p. 687).

The deposited eggs are generally attached to a solid substrate, via the chorion stalks and a cement produced by the oviducal glands in octopods, or via the gelatinous envelopes in decapods. Similarly, in *Nautilus* (Willey 1897). As far as is known only the oegopsids produce floating egg masses released into midwater.



Textfigure 18.—A freshly deposited egg of *Loligo vulgaris* drawn in an optical medial section. 15 × natural size. 1: micropyle; 2: formative cytoplasm with egg nucleus; 3: chorion; 4: yolk; 5: plasmic layer surrounding the yolk.



Textfigure 19. — An egg of *Octopus vulgaris*, enclosed in the chorion. 22× natural size. Note the sausage-shaped outline of the egg; the first cleavage furrow is formed, and the 3 polar bodies are recognizable; note also the size relationship between the nutritive yolk and the formative cytoplasm. The chorion shows a thickening around the micropyle and, at the opposite end, an extension into a hollow, distally solid stalk, which is characterized by a slight expansion and a thickened wall close to its base.

1: micropyle, close to the animal pole of the egg; 2: formative plasm with egg nucleus; 3: chorion; 4: yolk; 5: cytoplasmic envelope of the yolk mass.

The general form of the eggs varies somewhat. In the sepioids and loliginids the eggs have approximately the shape of a hen's egg, the more pointed end corresponding to the micropyle. In oegopsids the eggs are almost spherical. In the octopods the eggs are rather sausage-shaped, often with slightly flattened poles (Textfig. 19).

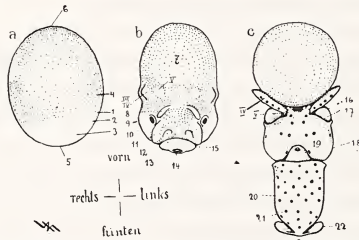
The eggs are always radially structured, i.e. in cross section they are circular, the egg axis corresponding to the prospective longitudinal axis of the animal. Slight deviations from this rule (as indicated by Watase for *Loligo pealei*, cf. Lang 1900, Mollusca, p. 445) are barely visible, and the bilateral symmetry of the germ is established only at fertilization and polar body formation.

I have not studied in detail the fine structure of the egg. From superficial observation one gets the impression that the formative plasm is sharply separated from the yolk, and that the bulk of the egg is pure yolk, made of a granular, translucent vitreous pulp which coagulates in sea water. But closer inspection shows that the normal cytoplasm continues as a very thin pellicle over the entire surface and also penetrates from the animal pole between the upper yolk granules. These are not separated from the cell body but are integrated in it even though they form a very compact mass.

The normal position of the cephalopod body was explained in Vol. 1 (p. 54). Upper and lower surface and right and left side are given by the normal swimming position of the adult animal. In the figures of dorsal and ventral views the head is generally directed upwards; in lateral views only if they are placed next to a dorsal or ventral view.—However, this is a conventional presentation dictated by practical aspects of description. The swimming position, especially of juvenile animals, is in fact different, the caudal end pointing more or less markedly upwards (Textfig. 30). Such a position was probably normal in the ancestral belemnoid forms before they had a

heavy rostrum. It can still be seen in *Spirula* (Vol. 1, p. 862) in which the rostrum load is no longer present (vol. 1, pp. 110, 517) so it shows the so-called morphological orientation (cf. Lang, Mollusca, 1900, p. 431). A strict application of the latter in cephalopod descriptions would impede visually profitable representations, however. It is advisable only when homologies with other molluscs and coelomates are discussed, especially regarding the anal, retroflexed body part and the early, disk-shaped stages of development.

In a "morphological orientation" of the egg or embryo, the animal pole, i.e. the formative yolk, is lying uppermost as in other coelomates (Textfigs. 6, 7, 18, 19) and this orientation is maintained for the subsequently arising organization. The animal will then be oriented head down (imagine Textfig. 20 inverted and compare them with Textfigs. 17, 25, 30), which is inevitable for a general comparison with other molluscs and with annelids (Textfigs. 8, 9, 10, 12, 15, 17). As I have shown earlier, this orientation cannot always be used for all other coelomates, in particular for chordates (*Biol. Zentralbl.* 1926, p. 39); in treating special groups one will have to consider their naturally established conditions of orientation, and in doing so one cannot always avoid arbitrary decisions in formulating generalizations. (Animals take little notice of our symmetry planes and axes!).



Textfigure 20. — Embryonic stages of *Loligo vulgaris* as an illustration of the prospective physiological orientation of the embryo. rechts = right, links = left, hinten = posterior

Ventral view. 15× natural size. Animal pole: posterior end. Vegetal pole: anterior end.

a) Stage with a thin, cap-shaped embryonic body (3) which has grown over the yolk to the line 1. 2: limit between embryo proper (3) and yolk sac envelope; 5: animal pole; 6: vegetal pole.

b) Stage showing the outer rudiments of major organ complexes. III-V: arm rudiments; 7: yolk sac; 8: right half of funnel tube rudiment; 9: eye; 10: statocyst; 11: funnel pouch; 12: gill; 13: prospective anus; 14: shell sac, still open; 15: muscular mantle.

c) Advanced embryonic stage. 16: eye vesicle; 17: primary lid; 18: cheek hump; 19: position of olfactory organ; 20: mantle sac; 21: chromatophore; 22: fin.

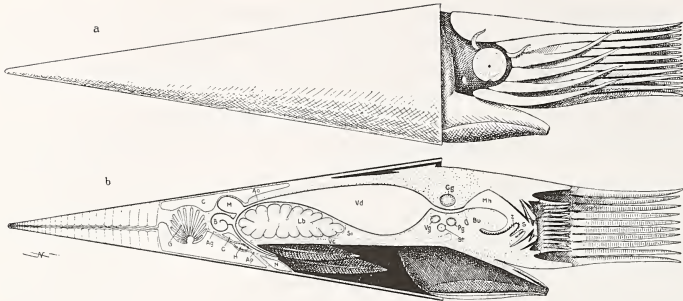
An orientation corresponding to the normal position of most adult forms (*Loligo*, oegopsids, *Sepia*) during swimming is termed physiological orientation, and when talking about embryos one will use the term prospective physiological orientation (Textfig. 20).

In this prospective physiological orientation the animal pole, i.e. the center of the blastodisc, corresponds to the posterior end, the vegetal pole, i.e. the rim of the blastodisc, to the anterior end; the longitudinal axis of the egg designates the longitudinal axis of the future animal. The eggs shown in Plates 1, 2, 15 and 24 are then viewed from behind, so that up and down, right and left are the same in the figures as in the embryos and in the future animals. The plane of symmetry is approximately determined by the first meiotic division, and the germ can then be orientated since the polar bodies indicate (roughly) the position of the first cleavage furrow (Pl. 24). They come to lie in its upper part or close by, either on the right or the left side. The egg nucleus becomes excentric, being displaced downward during the meiotic divisions.

II

Comprehension is greatly facilitated in a comparative study of cephalopod development when its archetypal, probably ancestral outcome is considered first, since originally all formative forces and ensuing developmental stages must have been focussed on this outcome, undergoing stepwise deviations only later. This original aim (p. 15) of ontogenesis was tentatively described in the first volume (p. 79) of this monograph, based on the methods of systematic morphology, with an attempt to provide positive evidence from observed facts; today we would have to add much complementary information from the domain of paleontological research, something we cannot do here. (I hope to have an opportunity to finish my monograph of the fossil tetrabranchiates, especially the nautiloids, to illustrate the special early history of cephalopods.) We simply repeat the picture given in 1921 in our Textfigure 21.

With some restriction (cf. Naef 1922, Fossil Cephalopods, p. 14) the archetype of all the younger cephalopods can be seen in an Orthoceras-like nautiloid, which is reconstructed in Textfigure 21. It is a conchiferan form with an outer, more or less obtuse or slender conical chambered shell, in other words, a "chambered limpet" (i.e. a tetrabranchiate) with a soft body built essentially like in the living *Nautilus*.



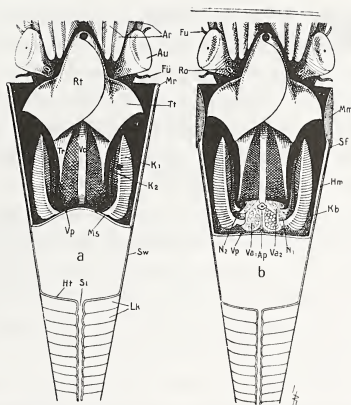
Textfigure 21. — Ideal cephalopodan prototype, constructed on the basis of comparative developmental history of dibranchiates, systematic morphology of cephalopod shells and the anatomy of *Nautilus*, and also based on the general concepts of molluscan morphology discussed above. — (From Vol. 1, p. 79. For the justification see Vol. 1, pp. 75-76).

a) Lateral aspect b) Left half of a hemisection. Note (in a) the numerous arms arranged around the mouth, the lateral ones having elbow-like bases surrounding the eye, some of them remaining shorter than the rest. The eye thus comes to lie in a depression, inside which it remains mobile but protected; the eye ball is constructed as a pin-hole camera. Behind the eye lies a papillar olfactory organ, situated between the conical funnel tube and the lateral funnel pouch.

The section (b) shows also the dorsal part of the funnel complex; it forms a gliding sledge, the nuchal attachment, adhering to the mantle and thus closing the dorsal mantle slit. Within the prehensile arm crown, a circle of buccal arms is visible anterior to the tips of the beaks. All the arms have their inner side differentiated with serial, glandular adhesive pads which act as very simple suckers. Inside the funnel tube, one sees the funnel valve which prevents reflux of water, and in the deepest part of the mantle cavity, the overhanging mantle cavity roof with the anus already removed from the mantle (cf. Textfigs. 10, 14 and 17) and the two gills of the left side. It is separated by a furrow from the visceral complex.

However, special differentiations and complications of the *Nautilus* organization (lacking in extant dibranchiates and probably also in their ancestors) are omitted in the homonomous and homologous parts; they are indeed considered secondary formations in *Nautilus*.

Textfigure 22 should be viewed correspondingly; it provides an interpretation of the most important conditions regarding the mantle cavity roof of *Nautilus* (Textfig. 11) and the corresponding parts of dibranchiates, placing emphasis on those processes that originally must have prepared ground for a transformation of tetrabranchiates into dibranchiates, thus bridging the deep gap between the two. The aim is an understanding of the ontogenetic processes, not a contention or conjecture (hypothesis) on the when and how of phylogenetic transition, i.e. under what conditions and in what combination the changes occurred.



Textfigure 22. — Mantle cavity aspects in an ideal protocephalopod of *Orthoceras*-like morphology (a), and in a hypothetical form which would have been transitional towards the dibranchiates (b); both illustrating the deviations from *Nautilus*-like conditions (see also Textfigs. 11 and 29). From Volume 1, page 85.

The ventral half of the shell is removed, along with the ventral half of the mantle, the cut edges being fully exposed. The funnel is shaped as in *Nautilus*; in (b) the lobes would fuse during postembryonic development to stabilize the tube. The posterior edge is drawn out into a pair of "funnel corners" marking the insertion (inside) of the septum and the origin of the retractors. In (a), the latter taper out in the visceral musculature (shell muscle), in (b) they extend directly to the shell. 2 pairs of gills lie in the mantle cavity; The mantle cavity roof (abdominal complex) is not visible in (a) since it is slanting forward from the ventral mantle furrow (or ventral mantle insertion: cut edge) as in *Nautilus*; in (b) it is shifted like in dibranchiates and therefore visible. The ventral mantle furrow lies more posteriorly than the dorsal one (Textfig. 15). — (b) shows the development of an incomplete muscular mantle (Chapter 2); both figures illustrate the positional relationships of the prominent eyes with the arm bases, the funnel, the mantle rim and the olfactory organs. — Ar: arms; Au: eye; Fu: ocular palp; Ro: olfactory organ; Mr: mantle rim; Mm: muscular mantle; Sf: shell fold; Hm: membranous mantle; Kb: branchial band; N₁: opening of the anterior kidney sac, functioning also as a sexual outlet; N₂: opening of the posterior kidney sac; Va₁ and Va₂: venous appendages (visible through the visceral integument) of the anterior and posterior kidney sacs; AP: Arteria pallialis medialis (cut off); Vp: Vena pallialis posterior; Ms: mantle section; K₁: ventral (posterior) gill; K₂: dorsal (anterior) gill; Vc: Vena cava; Tr: funnel retractor; Rt: funnel tube; Hf: shell epithelium; Si: siphuncle; Lk: gas chamber; Sw: shell wall.

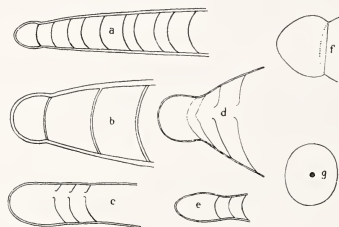
In *Orthoceras* the mantle cavity roof was probably overhanging, similar to *Nautilus* and archaic gastropods, so that its surface does not become visible after simple removal of the mantle. It is displaced in the hypothetical form b so that the connection with the mantle lies behind the connection with the trunk, thus exposing a situation that becomes visible in *Nautilus* only after further preparation (Textfig. 11).

It will of course remain impossible to know much about the embryonic development of very ancient, *Orthoceras*-like tetrabranchiates. But the growth mode of conchiferan shells still provides some information on the ontogenesis of these important parts even in fossil forms, since the juvenile stages remain conserved in the finished shells so that the successive phases of their formation can be read from the growth stripes (cf. Vol. 1, p. 858). Finally, some fortunate events have made available a number of very young orthoceratid stages (Textfig. 23).

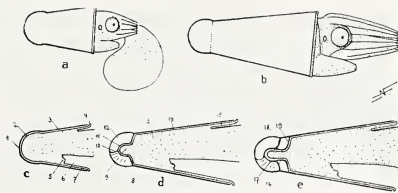
77 The similarity of these formations with shell nuclei of *Nautilus* and of chambered dibranchiates permit some generalizations about development of typical cephalopod shells and associated soft parts, so the assumed picture of embryonic development in *Orthoceras* (Textfig. 24) should not be too far removed from the real process. From the outset the relationship of the animal to its shell is the one typical for conchifers. There is no reason to assume special modifications in shell or mantle rim structure prior to the onset of septal formation. The septa appear to form a unit, together with the septal necks (which can be viewed as caeca), being special differentiations of the hypo-

78 stracum.

These relationships are suggested here mainly to facilitate understanding of the following points. The development of the cephalopodium is thought of as essentially similar to that observed in *Nautilus* and dibranchiates, but without the special differentiations of these (e.g. adjustment of the arms to the shell form in *Nautilus*). Nothing



Textfigure 23. — Longitudinal (grinding) sections of very young orthoceratid shells: a-e after Pocta (1902), f-g after Clarke (1893). From Volume 1, page 88. Note the solidly calcified, variably shaped embryonic chamber, which always has a vesicular, swollen aspect, the unequal apertural angle, the only partly calcified and conserved septal necks, and the differently spaced septa. Forms like (d) should probably be interpreted as belonging to creeping animals living like gastropods, or to pteropod-like swimming animals in which the head-foot was facing down. Such brevicone (primitive?) forms are always very small (cf. Textfig. 17a₁). f: lateral view; g: first septum.



Textfigure 24. — Hypothetical development of an orthoceratid (from Vol. 1, p. 89). About $6\times$ natural size. — a) Embryo prior to the formation of the first septum; b) Embryo with one air chamber (embryonic chamber); c) Posterior body end of a, in medial section; d) Posterior body end of b, in medial section; e) Formation of the second septum and septal neck. 1: shell apex (initial dome); 2: shell epithelium; 3: conical part of the shell; 4: mantle rim; 5: anus; 6: mantle cavity; 7: mantle; 8: prosipho, sagittal lamella; 9: fleshy siphuncle; 10: prosipho, main pillar; 11: initial caecum of the siphuncle; 12: embryonic chamber; 13: soft body; 14: shell epithelium; 15: nuchal attachment; 16: second septal neck; 17: first septal neck; 18: first shell septum; 19: second shell septum.

is known of the number and division of labor of the arms. The arm number was probably as high or even higher than in *Nautilus*, hence simplified in the present diagram.

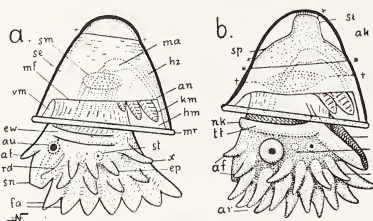
III

Unfortunately the embryonic development of recent *Nautilus* species is still unknown. Willey (1897) only describes the spawned eggs of *N. macromphalus* from the New Caledonian archipelago. (See Lang 1900, Mollusca, p. 444) A few firm statements are nevertheless possible, along with some well-founded presumptions. It would even be conceivable to construct a hypothetical embryology of these interesting forms, based on a) existing knowledge of general developmental conditions, egg form and size, b) ontogenetic data of the shell extracted from growth lines and other growth conditions, c) a methodical comparison of the organization of *Nautilus* with the known ontogenesis and organization of dibranchiates, assuming that homologous formations are derived from similar anlagen (p. 18).

Thus the considerable egg size (pp. 70, 71) already permits the assumption that cleavage must have been similar to that observed in dibranchiates. This assumption is based on the realization that cleavage in dibranchiates is mainly determined by the particular yolkiness of the teleolecithal egg, which leads quite mechanically to a mer-

oblastic-discoidal process and places the micromeres in special positional relationships to one another within the flattened blastodisc. Furthermore, it appears quite clearly that, like dibranchiates, *Nautilus* cannot have veliger stages (not even inside the egg capsule), but must develop directly into a tetrabranchiate. The size of the soft body in hatchlings must correspond roughly to that of newly-hatched *Sepia* (Pl. 20); given the gas volume contained in the shell, the overall volume should be considerably larger (cf. Vol. 1, p. 57). The shell size at hatching can be derived from other indications as well:

A peculiarity of the shell nucleus provides some information on the growth stage



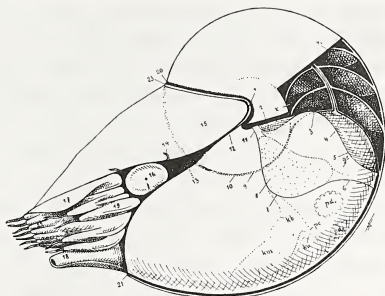
Textfigure 25. Comparison between an ideal protoconchifer(a) and a hypothetical *Nautilus* embryo at a homologous stage.

a) This figure can be compared to Textfigure 17 b and g; it shows the bluntly rounded, typical juvenile shell. The subdivision of the head-foot approaches the conditions known from cephalopods, in order to permit direct comparison with the corresponding parts of the head-foot organs in other molluscs. The number of gills is arbitrarily considered (above the known dimeric level) to be three pairs, but it could well be more or less than that if we attempted to define a real ancestor. The line x.....x marks the end of a distinct, original shell part (cf. Textfig. 13 e) that was further enlarged by concentric apposition.

sm: insertion of shell muscle; se: shell epithelium; mf: mantle furrow; vm: anterior mantle cavity; ew: suprapedal pad; au: eye; af: ocular palp; rd: radula pouch; sn: snout; fa: pedal appendages; ep: epipodial palps; x: similar palp instead of left funnel tube rudiment; mr: mantle rim; ma: posterior mantle cavity; km: gill; an: anus (situated in primary position); hz: heart; ma: stomach.

b) This figure shows the real shell nucleus of *Nautilus pompilius* in a sagittal section; the excentric growth, which will later generate shell volution, is not yet conspicuous. The first septum is formed and contains the siphuncular caecum, which is connected to the primordial shell (x); the line *.....* marks the stretched suture line, i.e. the connection of the septum with the actual hypos-tracum. This line is also the upper limit of the annulus, i.e. of a zone of fusion of the shell epithelium with the shell, to which the shell muscle insertion belongs, and which produces a special variant of hyostracum, similar to the corresponding formations observed in other conchiferan molluscs. The line +.....+ marks the lower limit of the annulus.

The head-foot architecture is slightly simplified according to adult structures, the individual parts being reduced to their rudimentary condition (as observed in dibranchiates), and the snout is not yet figured as embedded in the arm complex. The embryo would still have a very large yolk sac, due to the presence of which the various parts of the head-foot could be pulled apart to some extent (cf. Pls. 4 and 9). nk: nuchal attachment; tt: funnel pouch; af: ocular palps; ro: olfactory organ; tr: funnel tube with funnel valve.



Textfigure 26. — (From Vol. 1, p. 59; one half natural size).

Nautilus pompilius in lateral view. The shell is partly opened to expose the soft body, and the last few chambers are shown in hemisection. One can recognize the fleshy siphuncle and the siphuncular tube of the shell. y: lower side of the penultimate septum; x: upper side of the penultimate septum. The last septum is still thin and incomplete. 1: free dorsal mantle rim; 2: posterior limit of the annulus, accompanying the insertion (lobe line) of the last septum to the shell wall; 3: lateral lobe of the line; 4: posterior wall of the visceral sac, lying against the last septum; 5: origin of the genital septum; 6: anterior limit of the annulus; 7: anterior rim of the insertion of the head-foot retractor (8); 9: dorsomedial limit of the mantle sac, depressed by the older parts of the shell (10); 11: narrow, dorsal part of the annulus; 12: free mantle rim; 13: funnel pouch; 14: ocular palp; 15: hood; 16: eye; 17: part of the hood formed by the second arm pair; 18: funnel; 19: brachial palps; 20: limit of the black substance (dorsal shell rim); 21: ventral shell rim; 22: prehensile arm; 23: dorsal mantle rim; pd₁: upper pericardial gland; pd₂: lower pericardial gland; pc: anterior limit of the pericardium and origin of the mantle; kb: brachial band; kv: brachial vein; Km₁: upper gill; Km₂: lower gill. — This figure is essential for the assessment of archetypal relations between the animal and its shell.

attained by the young *Nautilus* when it hatches from the egg capsule (cf. Vol. 1, p. 554). Following a slow increase in embryonic chamber volumes, one finds traces of a sudden interruption of this growth process. In *N. pompilius* the 7th chamber (or the 6th or 5th chamber in other species) is strikingly narrow, whereas subsequent chambers again show normally increasing volumes. The narrow chamber can only be the one formed after hatching, like that observed in *Sepia officinalis* (loc. cit.).

It is not intended to develop here a complete hypothetical embryogenesis of *Nautilus*, although such an attempt could form a useful test for the accuracy of assumed morphological principles; there is indeed hope that sooner or later such a construction can be verified directly. It is merely for a facilitation of comparisons that a hypothetical embryonic stage of *Nautilus* (cf. Pl. 17) is given here along with an ideal young protoconchiferan. The picture of course is not freely invented, but built from a methodical application of all the known facts that can serve as guides. In par-

ticular it is based on the law of conservative preliminary stages, i.e. on the realization that similar parts must arise from even more similar anlagen.

Moreover, the comparison of tetrabranchiates and dibranchiates should be facilitated by the reproduction of two pictures of *Nautilus* from Volume 1.

These pictures show nearly adult stages, and for a comparison with embryonic stages of dibranchiates the reader will have to use some imagination to get a picture of homologous phases in the organs in *Nautilus*. At any rate, given the principal aspects explained in the Introduction, one will not expect to see a recapitulation of finished *Nautilus* (or ancestral) stages in dibranchiate embryos and larvae, but formations only similar to the assumed homologous preliminary stages of ancestors so far as they have conserved archetypal conditions. Textfigure 26 is intended mainly to illustrate the insertion of the entire, normally formed soft body of *Nautilus pompilius* in the shell, something for which rather unfortunate pictures have been used in the past. These pictures show the animal as rather deformed and thus lead, especially for paleontologists, to quite erroneous representations (relation of annulus, shell muscle and suture line).

A more general overview of the anatomy of *Nautilus* and its relation to dibranchiate anatomy is given in Textfigure 27. Here some general features are only indicated:

I. General conchiferan features: 1) A particularly well-differentiated shell epithelium covers a large part of the visceral sac and secretes the material for the shell, which is built partly by surface growth (in thickness), partly by marginal (linear) growth, producing ostracum and hypostracum, respectively. 2) The marginal parts of the shell epithelium belong to the mantle, i.e. to an integumental fold surrounding the mantle cavity; in b this fold is visible in its typical form only dorsally in the median section (at Nk). 3) The gills are situated laterally in the mantle cavity roof, which shows an altered, longitudinal orientation in b. 4) The cephalopodium is linked to the visceral sac by a neck-like, thick middle piece (cf. p. 63) through which the fore-gut passes (Vd). 5) The cephalopodium shows a rich organization of muscular and sensory parts.

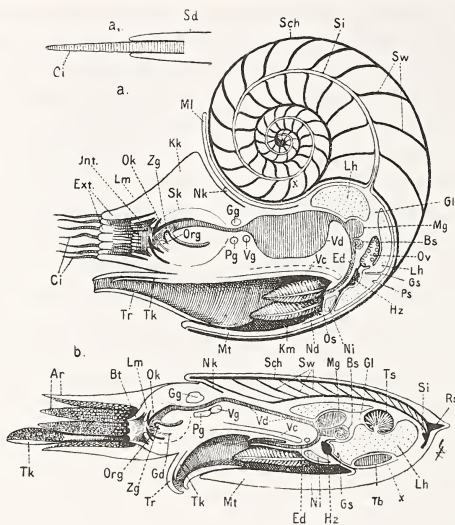
II. General cephalopodan features: 1) The shell epithelium is particularly well differentiated in its greater part which produces the hypostracum; it provides a) normal strata that increase the thickness of the marginal parts of the shell (living chamber), b) the annular layer deposited on it during advancement of the soft body, c) the supporting ribs and septa deposited on the annular layer along the suture line, d) the septal necks, the first ones being closed caeca, the subsequent ones forming open funnels

each cemented to the preceding one. 2) The anus is more or less markedly displaced towards the middle piece. 3) The mouth is buried in the center of the cephalopodium, in other (more precise) words: the snout part (including inner and outer lips) of the cephalopodium appears from above to be submerged into the bulk of the remaining parts, by a process still observable in embryonic development, as will be shown. 4) The muscular, motor and sensor appendages of the cephalopodium are richly organized and subdivided essentially in a funnel and an arm complex. 5) The funnel complex occupies the mantle slit, at the transition between middle piece and cephalopodium; it comprises: *a*) the ventral funnel tube with a funnel valve, the tube being formed by two-folded lobes in *Nautilus*, *b*) the nuchal attachment which adheres dorsally to the mantle, *d*) the connected lateral funnel pouches, which are united with the funnel tube at the funnel corners on either side, the enclosed spaces remaining separated by the "funnel septum". The latter continues posteriorly to the middle piece (to the shell in dibranchiates) in ridge-like muscles projecting into the mantle cavity; these are the funnel retractors. (On the combined function of these parts see Vol. 1, pp. 83-84, 100-102, 123). 6) The arm complex is subdivided into an outer crown of prehensile arms and an inner circle of buccal arms (buccal funnel) surrounding the mouth like a third lip; in dibranchiates it is more or less rudimentary. In *Nautilus* the outside of the arm crown bears additional palp arms (Vol. 1, pp. 61-62) as shown in Textfigure 26 (14, 19). In this same area of the lateral cephalopodium faces lies the large, pedunculated eyes, set between the arms and the mantle (shell) rim; behind the eyes a short stretch of sensory epithelium lying in a pit-like depression is associated with the statocysts, 83 the latter being completely covered by the integument. Both are lying close to the corner between funnel tube and funnel pouch (cf. Textfig. 28).

III. Special features deviating from the archetypal cephalopod pattern are present already in *Nautilus*:

Spiral coiling results in a "compression" of the soft body along the dorso-ventral axis, the connected parts of the mantle, the nuchal attachment and the dorsal arms having apparently undergone a secondary adjustment. (The whole arm complex is shown diagrammatically, with reduced arm number and very similar aspect of individual arms in the outer and inner circles 'cf. Vol. 1, p. 65'.)

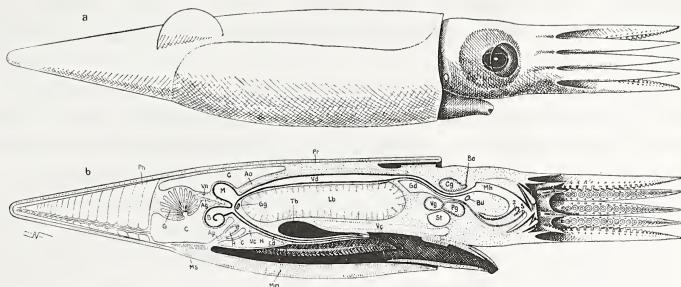
84 Special attention should be given to the difference between the respective features of "chambered limpet" tetrabranchiates (protocephalopods) and dibranchiates, the latter being represented in b by a very special variant. Here we emphasize only the typical features: In dibranchiates the shell is covered by an integument (shell fold) and is



Textfigure 27. — Schematic hemisections of *Nautilus* (a) and *Sepia* (b) as guides for a comparison of tetrabranchiate and dibranchiate organization. Lm: labial membranes (outer lip and inner lip); Ok: upper beak; Zg: tongue; Kk: hood; Nk: nuchal attachment; Ml: dorsal mantle lobe; Sch: shell; Si: siphuncle; Sw: septa of gas chambers; Gd: poison gland (outlet); Gg: cerebral ganglion; Pg: pedal ganglion; Vg: so-called "visceral ganglion" or pleural ganglion; Vd: foregut; Vc: Vena cava; Ed: hindgut; Mg: stomach; Bs: caecum; Ov: ovary; Lh: body cavity (coelom); Gs: genital septum; Ps: pericardial septum; Hz: heart; Ni: kidney; Km: gill; Mt: mantle; Int: sheaths of inner arm crown; Ext: sheaths of outer arm crown; Ci: cirri; Ar: prehensile arms; Tk: tentacular club; Bt: buccal funnel (lappets); Tb: ink sac; Ts: testicle; Rs: rostrum; Os: "osphradium"; Nd: nidamental gland; Org: subradular organ; Gl: gastrogenital ligament.

thus enclosed in an epithelial shell sac consisting of a primary and a secondary shell epithelium. The latter lies on the outer side of the shell and adds strata that are generally called periostracum; the rostrum (Rs) is part of it.

A much more important modification is the replacement of the ventral part of the shell and of the connected integumental mantle (Mt) by another form of mantle, which is not homologous to the former, namely the muscular mantle (cf. Vol. I, pp. 93-95, 108). The shell has given way to it and regressed to the posterior end, providing the necessary base for the fixation of this muscular organ. As a consequence the mantle



Textfigure 28. — Ideal prototype of dibranchiate (from Vol. 1, p. 91), to be opposed to the primary prototype of cephalopods in general (Textfig. 21). The figure is constructed from a methodical comparison of Textfigure 21 with all dibranchiate types at both adult and juvenile stages; it can thus be considered as the general norm of dibranchiate architecture. However, the fins should be figured in more posterior position (like in Textfig. 30).

a) Lateral view. b) Hemisection. Note the relationship between the membrane-covered shell and the muscular mantle (Mm), the position of the fins, the shape of the mantle rim, the shape of the primary eye lid and of the iris, the arrangement and interrelation of the arms the arrangement of the suckers on the prehensile and buccal arms, the structure of the outer and inner lips, of the beaks and the radula! Note also the structural features of the shell shown in sagittal section, of the dorsal and ventral parts of the mantle cavity, of the funnel tube! — Ph: phragmocone; Pr: proostracum; G: testicle; C: coelom; Ms: mantle septum; Ap: Aorta posterior; H: heart; vc: Vena cava; N: kidney; Ed: hindgut; B: caecum; Ag: arteria genitalis; Vn: Vena genitalis; M: stomach; Ao: Aorta anterior; Gg: Ganglion gastricum; Tb: ink sac; Lb: liver; Vd: foregut; Gd: poison gland; Vg: "visceral" (parietal) ganglion; St: statocyst; Cg: cerebral ganglion; Pg: pedal ganglion; Bo: upper buccal ganglion; Bu: lower buccal ganglion; Mh: buccal cavity; Z: tongue; S: subradular organ.

cavity penetrates deeply into the visceral sac, pushing the mantle cavity roof against the body in downward orientation.

Note also in b the appearance of suckers and an ink sac along with the disappearance of one pair of gills (the upper one in a).

IV

Textfigure 28, which illustrates the archetypal organization of an adult dibranchiate, provides a more general presentation of the morphological conditions of this group. Our introductory considerations suggested that the general trend of

dibranchiate embryos, once they have 'given up' aiming at a general tetrabranchiate organization (Textfig. 21), is a deviation in the new direction of primary dibranchiate features.

Here we wish to emphasize the essential features, which will be achieved in the special dibranchiate development, meaning also those from which the various ontogeneses will depart along with conserving more or less distinct reminiscences of archetypal conditions (i.e. from which they apparently deviate by adopting what appears as a secondary condition compared to the more general, more ancient norm; this secondary condition can here be defined in a phylogenetic formulation):

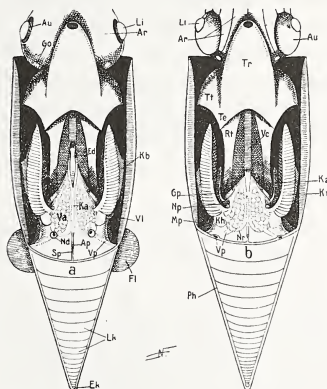
The dibranchiate type is characterized by a marked predominance of active and aggressive elements of organization against the passive and defensive ones, the dibranchiate cephalopod being the only invertebrate type having successfully competed with the vertebrate type in the open sea since paleozoic times. Eyes, arms, statocysts and funnel apparatus have achieved a huge increase of efficiency compared to the older tetrabranchiates, and the relationship between the visceral sac and the shell is thoroughly modified, resulting in a more active swimming apparatus.

In this process the shell has become entirely covered by an integumental fold, the so-called shell fold, the musculature of which has differentiated a special locomotory and steering organ, the fins, which are inserted, with mobile bases, on the outside of the shell complex (cf. Naef 1922, Fossil Cephalopods, p. 24). Starting from the soft mantle rim (cf. Textfigs. 13 and 43) a muscular plate, the so-called muscular mantle, extends ventrally and tapers off dorsally on either side anterior to the shell rim, the latter staying behind correspondingly. The funnel tube is ventrally closed due to the solid fusion of the two lateral lobes, and it is relatively smaller, as are the funnel pouches, compared to the mantle which now forms the counterpart of the funnel as part of a novel pumping device. A closed, contractile circular fold surrounding the eye ball forms the primary lid; the pore of the camera obscura type eye is closed and builds a spherical lens comprising an outer (smaller) and an inner (larger) segment. Access of light is regulated by an iris fold. The palp arms or their homologs have disappeared; the prehensile arm number is reduced to 10; instead of adhesive or sensory papillae each arm has a row of suckers accompanied by two rows of palp-like appendages. The number of buccal arms is reduced to 8, and in each of the arm circles the arms are more closely united by an umbrellar membrane.

In the mantle cavity the anterior pair of gills (i.e. the pair lying dorsally in *Nautilus*) has completely disappeared along with the associated pair of renal sacs. The

87 corresponding coelomic issues, the gonoducts, are therefore independent, but do not much deviate secondarily from the pattern observed in *Nautilus* (as far as their relation to the conserved parts is concerned).

The whole mantle cavity roof is shifted, now slanting ventrally (cf. Textfigs. 21 and 29). This of course relates to the development of the muscular mantle, along with which the mantle cavity must have penetrated deeply into the visceral sac. The actual



Textfigure 29. — Archetypal conditions in the mantle cavity of dibranchiates (a), illustrated by means of a constructed form that suggests a transition from the tetrabranchiates (b). From Volume 1, page 101. See also above, Textfigure 22.

Both these ideal figures are given as if drawn from preparations after removal of the ventral part of the muscular mantle; in (b) the composition of the head by derivatives of arms (Ar) is indicated (see the text; cf. Textfig. 90). In (a) the head is rounded, with (naturally) open primary lids. Note prominent eye lenses (Li), and olfactory organs (Go) in their typical position.

Tr: funnel tube; Tp: funnel pouch; Te: funnel corner; Rt: funnel retractor; Vc: Vena cava; K₂: the anterior, dorsal gill which is missing in dibranchiates; K₁: the ventral gill, which is larger in *Nautilus* already (Textfig. 27).

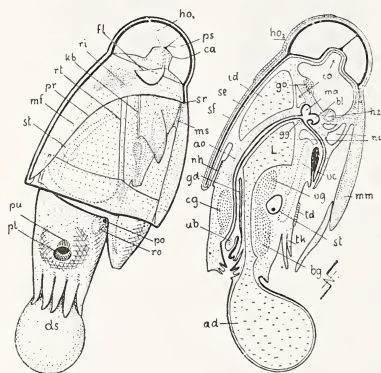
Gp: genital pore; Np: kidney pore; Mp: part of the original mantle lying on the marginal zone of the shell; Kh: branchial heart; Nr: kidney sac; Vp: Vena pallii posterior; Ph: phragmocone, visible through the shell cover.

The area of the mantle cavity roof has the position typical for dibranchiates only in (a). Ed: hind-gut, with anal papilla (quadripartite slit); Ka: Musculus rectus abdominis; Va: venous appendages; Nd: nidamental glands; Ap: Arteria pallii posterior; Vp: Vena pallii posterior; Sp: Septum pallii medianum; Fl: fin; Lk: air chambers.

This Textfigure, considered together with Textfigure 22, provides an idea about the modifications of the mantle cavity that can be assumed to have occurred in the course of phylogenesis, and about the only conceivable relationship between tetrabranchiates and dibranchiates.

primary muscle mantle has largely degenerated. In the dibranchiates only a few remnants are recognizable, especially in the area of the nuchal attachment. The region of the anal papilla is drawn out anteriorly along the cephalic vein; posteriorly appears the typical ink sac (Pl. 7 and 18), encircled by the two bases of the *Musculus rectus abdominis* (Ka) which tapers off posteriorly towards the issue of the *Arteria pallalis* posterior and the root of the mantle septum (sp).

To conclude this general overview we use the picture of an ideal primitive dibranchiate at an advanced embryonic stage (Textfig. 30). It will allow one to imagine the process by which the adult stages of Textfigures 28 and 29 were reached, along with a derivation of all the larval organizations in living and fossil cephalopods. Thus 88 it provides the widest possible insight into their morphology, and one can easily imagine that originally all dibranchiate ontogeneses aimed at the realization of such a stage, only afterwards taking their own path at an earlier or later point of diversion.



Textfigure 30. — Ideal prototype of an advanced dibranchiate embryo, to be compared with the somewhat less advanced stages of a protoconchifer and protocephalopod, respectively (Textfigs. 24 and 25), and also with Textfigures 63, 94, 100 and 117. — Further explanations with Textfigure 55.

CHAPTER 3

The Typical Process of Early Embryonic Development in Cephalopods (Dibranchiates)

Contents: 1st period: maturation, fertilization, spreading of the blastodisc (p. 91), 2nd period: cleavage (p. 92), 3rd period: formation of germ layers (p. 96), 4th period: mesoderm grouping in preparation of outer organanlagen (p. 103), 5th period: folding processes in the embryo and the establishment of surface architecture (p. 107).

This chapter and the following one will describe the embryonic development of a dibranchiate cephalopod, based on special observations but limiting the description to the general, typical aspects and using pictures showing these aspects clearly.

The description follows a sequence of rather naturally defined periods of embryonic development, seven of which can be distinguished; they are not given equal weight and attention in our considerations.

The respective duration of these periods is very different indeed; it varies widely with temperature and with the special developmental conditions of the species. The norm chosen is generally *Loligo vulgaris*, the form most easily studied, or species with similar egg sizes. The temporal indications are only approximations and generally refer to the conditions observed in the aquarium tanks of the Naples Station during early summer. Room temperature at noon about 24° C, water temperature about 22° C.

The entire development then takes about 4 weeks; but this period can be stretched to 3 months when the eggs are very large (*Sepia officinalis*) and when the aquarium water temperature is considerably lower (January to March). Small eggs, on the other hand, can have a much shorter developmental duration, especially when the water

temperature is high (cf. Grenacher 1874). I have not made detailed studies on these
89 variations, because they are relatively time-consuming with the most frequently investigated forms (except *Loligo vulgaris*), and they were of only limited interest compared to the more important questions I had to deal with. For *Sepia officinalis*, for example, I obtained only rarely greater numbers of eggs at comparable developmental stages that could have provided the basis for precise records of development over 2–3 months. To ascertain sample quality, a considerable number of freshly collected eggs have to be sacrificed without providing any precise results. In fact one egg mass can be the result of the spawning activity of several individuals having laid their eggs at different days. During continued observations of a given egg mass, one may thus suddenly encounter much more advanced embryonic stages that prevent a reliable staging of an ostensibly 'homogeneous' sample. In general eggs spawned in the aquarium are not of high quality; they often die very soon or do not develop at all, so that particularly favorable conditions are needed to follow the whole development under experimental conditions. This is best achieved with young egg masses of *Loligo vulgaris*, in which individual embryos differ by no more than one day in age, or eggs of *Sepiolo*, which are always found in very limited numbers, but which allow one to identify developmental stages through the relatively transparent envelopes, although details of embryonic development are not easily observed under these conditions; at least they require no special care. I did not know this beforehand, and given the other tasks at hand, I have not fully exploited this material to study the temperature dependence of embryonic development.

The following list gives an overview of developmental periods, based on the combination of notes on *Loligo vulgaris* made under the above-mentioned conditions; they are also valid for *Octopus vulgaris*, which could be studied only in high and late summer. Total duration of embryonic development in both cases about 28 days.

Developmental periods: 1st period: maturation, fertilization and spreading of the blastodisc $\frac{1}{2}$ to 1 day, 2nd period: cleavage to complete blastoderm (stage I) 2 days, 3rd period: germ layer formation, establishment of endoderm and yolk epithelium (stages II-IV) 3 days, 4th period: mesoderm concentrations and preparation of externally visible organ anlagen (stages V-VII) 3 days, 5th period: elevation of folds on the blastodisc with formation of externally visible organ anlagen (stages VIII-XI) 4 days, 6th period: secondary shifts and formation of typical dibranchiate topography (stages XII-XVII) 5 days, 7th period: linear growth of embryo into a viable young animal (stages XVIII-XX) 10 days.

For the period of cleavage the designation of stages is given by the number of blastomeres. Subsequent stages are given the Roman numbers I to XX, I designating the complete blastoderm, XX the hatchling (no yolk sac left, or only an inconspicuous remainder present). These stages are chosen for the dibranchiates in such a way that 90 the same numbers correspond approximately to the same developmental stage in different species, notwithstanding the existence of heterochronic shifts in the different parts of the embryos. Using this numbering, developmental series can thus be viewed in parallel to compare any embryonic picture in one species with a corresponding picture in an other species; see for example, Plate 5, Figure 2; Plate 16, Figure 6; Plate 23, Figure 7.

The most advanced stages and hatchlings (XVIII-XX) are often barely comparable as whole animals, because certain processes that occur in the embryo in species producing large eggs may be postponed until free larval life in others. Furthermore, organs may become functional at very different levels of architectural differentiation, so that morphological and physiological correspondences are not occurring in parallel and the deviations can no longer be viewed as merely heterochronic shifts.

1st Period: Maturation, Fertilization, Spreading of the Blastodisc

With the exception of ovoviviparous argonautids, newly-laid eggs have not yet finished their maturation (but see Vialleton on *Sepia*); two polar bodies are extruded only after laying, the first one generally undergoing a further division. The orientation of the first division spindle, which is perhaps influenced by the newly-entered spermatozoid, indicates the direction and polarity of the symmetry plane, at least approximately.—I have not followed in detail the process of fertilization.—

Next follow the preparations for the first cleavage step (Pl. 24). They consist of a spreading of the formative yolk which up to that stage had been very concentrated, bulging into the nutritive yolk (Textfig. 18); it now forms a cap- or disk-shaped cover on the animal pole of the egg. Only after this spreading does the first cleavage start (Pl. 24, Fig. 4).

At its periphery the "blastodisc" always shows a limit that appears blurred due to the fact that it grades into the fine plasmic pellicle that covers the ovum. Sections

show that there is no distinct limit between the two components, since very fine cytoplasmic extensions penetrate between the yolk granules to reach deeper layers of the yolk mass.

2nd Period: Cleavage

In dibranchiate cephalopods cleavage is meroblastic-discoidal, probably as a mechanical consequence (as suggested earlier) of the telolecithal nature of the unusually large eggs. Other important features of dibranchiate cleavage are not as easily explained, however, especially the following three which place the cephalopods in a rather problematic, strict opposition to the other molluscs:

- 1) Cleavage is not strictly determinative or mosaic-like, at least in its later phase.
- 2) There are strong deviations within the class, even at early cleavage stages (difference between octopods and decapods, Plates 1 and 24).
- 3) The first cleavage steps are strictly symmetrical indicating a primary bilateral structure of the whole germ.

These three peculiarities are not independent from each other; indeed the first one is the prerequisite for the following two. So far as the individual blastomeres are not strictly fixed in their prospective determination, a shift in position, i.e. a modification of cleaving order is possible, which may explain the considerable differences in cleavage processes within the class and also the fundamental divergence of cephalopod cleavage from that of all other molluscs.

For a long time I found it problematic to derive the cleavage, especially that of decapods, from the typical spiral cleavage of other molluscs and annelids, or to find an unequivocal, special morphological relationship between these two types of cleavage. I even considered the question whether perhaps the spiral cleavage could be a secondary phenomenon in molluscan ontogenesis, so that the cephalopods would represent the primary cleavage type and thus would not have to be derived from the spiral cleavage. But I have neither found detailed arguments to derive cephalopod cleavage directly from spiral cleavage in a systematic way, nor is the inverse possible, and I have therefore come to the conclusion that an entirely novel mode of cleavage has evolved once the strictly determinative cleavage mode was given up.—This idea

imposed itself during my observations of octopus cleavage, and considering the markedly irregular cleavage in later decapod stages that show numerous individual variations.

In *Octopus vulgaris* (chapter 12), barely one 16 cell stage looks exactly like others, and at the 32-cell stage it is generally impossible to reconstruct the preceding cleavage steps to define the origin and homology of individual blastomeres. Thus the cleavage process does not produce a strictly ordered cell material; the germ, i.e. the blastoderm appears (with some restrictions) as a homogeneous cell aggregation whose individual elements are of more or less contingent (lawless) origin, their prospective significance being determined only by the achieved positional relation to the whole.

Under such circumstances a modification and reorganization of the typical cleavage process is possible, and there is no reason to derive the existing regularities in typical cephalopod cleavage directly from the spiral cleavage that can be assumed to have existed in the archemolluscs.

The first cleavage furrow (Pls. 1 and 24) marks the symmetry plane of the future animal. This step produces only an incomplete division of the (meroblastic) egg, indeed of the formative plasm, since only the blastodisc is divided in two, not its continuation, i.e. the plasmic pellicle covering the yolk. The orientation of the second cleavage furrow is nearly perpendicular to the first, but it is slightly slanting downwards from the central point of the blastodisc, so that the resulting 4 blastomeres are of slightly unequal size: The lower two meet the central point of the blastodisc with slightly acute angles, the upper ones with slightly obtuse angles (Pls. 1 and 13).

The orientation of the germ can thus be seen unequivocally and does not need to be verified by the somewhat variable position of the polar bodies (p. 91): of the 4 cleaved cells, 2 can be identified as upper, 2 as lower, 2 as right and 2 as left cells solely by their respective forms.

The third division (Pls. 1, 13, 24) produces an 8 blastomere germ, the elements of which are still similar to the preceding 4 in their respective relation to the center of the blastodisc, and in that they are incompletely separated by furrows that reach only very little beyond the limit of the blastodisc. Each of the 4 blastomeres is divided into a more medial and a more lateral half, respectively (Pl. 24, Fig. 6). The relation to the yolk mass remains unchanged.—Otherwise some marked differences between octopods and decapods exist (Pls. 1 and 24).

It is only with the fourth cleavage step that 4 cells are completely divided and thus form a relationship with the remaining germ that can be compared with that of micromeres and macromeres, respectively. These fully individualized cells are derived from the 4 medial octomeres by centripetal division, whereas the lateral octomeres are cleaved again radially (Pl. 1, Fig. 4; Pl. 24, Fig. 10) so that 4 lateral macromeres lie on either side; together with the 2 medial ones on either side, a total of 12 macromeres obtains.

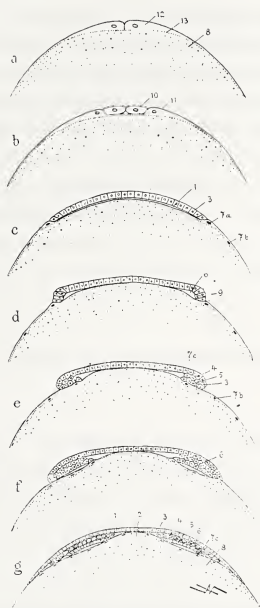
The 5th cleavage step produces 2 additional micromeres derived from lateral
93 macromeres on either side, which are added to the division products of the earlier micromeres, whereas the remaining macromeres (at least in octopods) again are cleaved radially; thus at the 32 cell stage there are generally 12 micromeres and 20 macromeres (Pl. 24). In decapods the relation is 14 to 18, because the posterior macromeres also produce micromeres.

This is the end of a pervasive regularity in cleavage processes, however; all the subsequent steps are rather variable. The micromere cleavages are strongly heterochronous, whereas the macromeres are partly giving off micromeres, partly dividing again as macromeres.

It is evident that the number of micromeres will soon exceed that of the macromeres, the result being a blastodisc similar to what is shown on Plate 1, Figure 7 and on Plate 24, Figure 15, i.e. a circle of macromeres surrounding a field of micromeres.

Apart from their respective position (marginal or central), the two types of cells differ in that the micromeres are separated from the yolk whereas the macromeres remain in continuity with it, i.e. they conserve the original connection (Textfig. 31). Apart from the details of their formation, these macromeres differ from the macromeres of other mollusc eggs by their incomplete separation, in that neither the yolk nor the surrounding plasmic pellicle are cleaved. In the following text they will be called the *yolk cells*.

The result of this cleavage process is a single-layered germinal disc (homologous to the blastoderm of other molluscs) as shown in Textfigure 31 c, and the whole germ corresponds morphologically to a blastula stage. Although it is generally devoid of an actual lumen the slit between the blastoderm and the yolk can be considered the homolog of a blastocoel. The blastoderm is closed by the yolk cells and the yolk, which form a morphological unit corresponding to the huge macromeres of other molluscan blastulae, with the difference that they are only incompletely divided in cephalopods.



Textfigure 31. — Diagrammatic cross sections through germinal discs in the course of cleavage and germ layer formation. a) The first cleavage furrow, separating left from right. b) Separation of the first micromeres. c) Complete blastoderm. d) Start of subduction of peripheral ring of blastoderm cells (gastrulation). e) Continuation of gastrulation; formation of a thickened rim of the blastodisc (Pl. 24, Figs. 17-18; Pl. 1, Figs. 9-10) by cell proliferation or folding of mesoderm. f) Gastrula stage with broad mesoderm ring below the ectodermic edge of the germinal disc; the yolk cells also shift towards the center. g) Fusion of the germinal layers with the yolk organ, at the right and left sides. Closure of the blastopore. Separation of "mesoderm" and endoderm.

1: blastocoel; 2: yolk organ, closing the endoderm mediodorsally; 3: lateral blastopore lip; 4: "mesoderm"; 5: endoderm; 6: lateral part of blastocoel (blastopore lip); 7 a, b, c: yolk cells; 8: yolk; 9: overgrown or tilted endoderm cells; 10: micromeres; 11, 12: macromeres; 13: limit between nutritive yolk and formative cytoplasm.

The interior cells of the blastoderm are not always of equal size; individual cells or groups of micromeres can become distinct in their respective size and arrangement, or in their cleavage pace; such groups show symmetric positions. A peculiarity that might be of morphological significance is the fact the interior cells in the center of the

germinal disc are not strictly adjacent to one another, but leave more or less regular gaps that persist for shorter or longer periods, sometimes up to the formation of the germ layers. Probably this formation of gaps is of no special interest to systematic morphology; it could indeed be a merely mechanic consequence of the great yolkiness by which the coherence of the germinal disc might be loosened, as if torn apart (cf. *Octopus* and *Argonauta*).

At early stages the yolk cells form a simple circle surrounding the entire germinal disc, but subsequently they divide also in radial direction; the elements given off centripetally do not always become clearly separated from the yolk. Thus the limit between yolk cells and disc cells is blurred, at least in some places.

3rd Period: Formation of Germ Layers

Germ layer formation raises special difficulties for the morphological interpretation of actually observed processes; it will be only outlined here, to be taken up again later when the formation of mesodermal and endodermal organs will be described. Here we need only a basis for the understanding of the development of surface structures.

The morphological analysis of sections and whole-mounts and of preparations made by mechanical denudation of cell material is difficult and time-consuming, so I consider as the foremost task for an introduction to provide a diagrammatic presentation, based on my own observations, that shows the ideal, likely typical process of germ layer formation, as given in Textfigure 31.

In the area where the interior cells are in contact with the marginal cells, subsequently a sort of congestion occurs, as if the marginal cells would not give way to the growing blastoderm; the result (Pl. 13, Figs. 6-7; Pl. 24, Fig. 17) is a more or less distinct shearing or folding over of the compressed marginal zone (light-shaded in the pictures) by the adjacent interior part of the blastoderm, which sometimes shows a very sharply circular limit and represents the ectoderm of the now-forming, greatly modified "gastrula". The cells having been covered then represent the endoderm together with the yolk cells. Such a process of shearing over, by which more centrally located cells move over more peripheral cells (with or without conservation of their

epithelial arrangement) is recognizable in all dibranchiates. During this process the yolk cells, at least the innermost, are covered by the shifted part of the germinal disc; the resulting change can be compared to or derived from an invagination (Textfig. 31).

95 Along with this process one observes a more or less marked loosening of the blastoderm, some cells leaving the epithelial complex to become located between the ecto-
96 derm and the endoderm. Since the constitution of the endoderm is not a strictly epithelial one, these ostensibly mesenchymal cells generally cannot be sharply distinguished from the endoderm; this leads us to the concept of the mesendoderm (Korschelt 1892).

The multilayered condition of the marginal zone of the germinal disc is not always continuous, but more like a ring-shaped string of pearls (Pl. 1, Fig. 9; Pl. 24, Fig. 17), which is due to the concentration of cell proliferation at certain points; sometimes (Pls. 1 and 2) a distinct gap remains at the posterior midpoint of the ring which closes down only later. It marks the future anal site.

As indicated above, the ectodermal part of the germ layer loses its marginal contact with the mesendodermal part and continues to expand (Textfig. 31 g) independently as if it aimed at a full enclosure of the yolk mass. In this movement the endoderm lags far behind, although it participates to a certain degree in this epibolic process. A "mesodermal" layer of cells, which is not very distinct, follows behind the ectoderm. In contrast, the yolk cells are drawn entirely underneath the germinal disc, generally prior to the onset of the epibolic growth of the ectoderm across the yolk surface; this retraction of the yolk cells enhances the impression of a modified invagination.

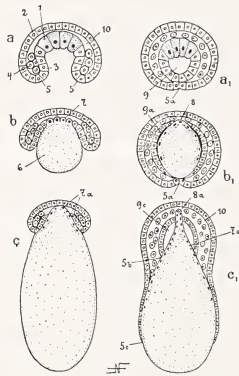
What makes this form of germ layer formation so different from a true invagination is the conduct of the yolk and yolk cells. The considerable volume of this complex makes its "invagination" into the ectodermal part of the blastoderm mechanically impossible, so that the blastoporus cannot be closed normally. As in bony fish embryos, the yolk complex projects from the blastoporus like a huge plug; the blastoporus appears only as a fine slit at the periphery of the now multilayered germinal disc.

The way in which this anomaly is compensated during early cephalopod development differs from that observed in yolky fish embryos, and it is out of the question to view the partly similar formations (yolk sac) as morphologically corresponding structures even in the widest sense. For the blastoporus of chordates lies on the prospective-morphological dorsal side, whereas in cephalopods it lies on the ventral side (cf.

p. 73). In the latter case the method by which the embryo deals with the yolk mass is much clearer: it starts from the blastopore edge. (But see *Zool. Jahrb.* 1927, p. 30).

If our general idea is correct, as seems likely from an immense number of facts, and if morphologically Textfigure 31 f is a cross section, then a process must ensue which corresponds to a fusion of the lateral blastopore edges, of course hindered and
 97 modified by the yolk mass. This process is apparently represented by the tight adhesion of the lateral edges (Textfig. 31 g) of the germinal disc on the yolk surface, the continuity between ectoderm and endoderm being given up. The dissolved blastopore lip continues to strive, as it were, for completion of the mechanically inhibited fusion of its edges by making special compensatory adjustments. They can be understood using the diagrams of Textfigure 32.

Above (pp. 94, 96) the yolk mass has been considered, in terms of cell morphology, as belonging to the yolk cells, and the whole from now on will be termed the "yolk organ". The latter will be considered a specially differentiated part of the endo-



Textfigure 32. — Diagrams for a comparison of germ layer formation in cephalopods (c, c₁) with typical molluscs (a, a₁) via a hypothetical transitional form (b, b₁). — Note the transformation of the yolk-laden endoderm cells (1, macromeres) which are made into a yolk organ (6); this organ retards the normal blastopore closure (b) and finally inhibits it altogether (c) so that the endoderm and ectoderm appear to be forced open, to finally "react" by a sort of regeneration.

1: macromeres; 2: ectomeres; 3: normal endomeres; 4: mesenchyme cells; 5: blastopore edge; 5a: seam of closed blastopore; 5b: endodermic part of blastopore edge; 5c: ectodermic part of blastopore edge; 6: yolk organ (syncytium); 7: yolk cells; 8: position of primary insertion of the yolk organ in the endoderm; 9: archenteron; 10: blastocoel with mesenchyme.

derm that can be compared (ill-defined limits notwithstanding) with the macromeres of a typical molluscan gastrula after production of a number of more normal endoderm cells (Textfig. 7 f). At any rate the yolk organ belongs to the endoderm complex and indeed continues to suggest that relationship. Its subsequent development allows one to provide a more detailed justification of this view: I will show later on that the yolk organ can be viewed as an embryonic organ sorted out specially from the material of
 98 the embryonic liver. This means that the organogenetic relationship of the yolk is the same in cephalopods as it is in other molluscs, namely lamellibranchs, gastropods and chitons. In any case this organ remains for a long time in connection with the midgut anlage, the latter being constituted only after its separation from the yolk organ.

A morphological comparison of these processes with a normal germ layer formation will be facilitated by Textfigure 32:

The conduct of the yolk cells is of particular importance in this comparison; in the normal development (a) they are and remain in the epithelial complex of the endoderm and are directly integrated into the midgut anlage, in particular into that of the midgut gland or "liver". In the supposed transitional stage (b) the endoderm complex is still intact, but the yolk mass is so large that it can no longer be distributed among the daughter cells (macromeres) and the invagination of the huge yolk plug is greatly retarded. In cephalopods an epithelial continuity between the yolk cells and the other endomeres is no longer distinct at these stages; it is lost during formation of the germ layers, and the latter—together with the yolk—constitute the yolk organ; henceforth they deal with the utilization of the nutritive mass only and are no longer a part of the cell material from which the embryo is built. At early stages the yolk organ is involved, at least topographically and mechanically, in the closure of the endoderm complex at the animal pole, but subsequently it recedes and becomes a thin strand traversing the epithelium; finally the other endoderm cells draw together and pinch off the remaining strand and close the wounds (cf. Textfig. 50 at 23).

In cephalopods the huge yolk plug at the vegetal pole makes a normal blastoporus closure quite impossible. The ectoderm and the endoderm combine their actions to overcome the obstacle. The continuity between these two layers is dissolved and each of them joins closely the surface of the yolk organ (Textfig. 31f, g); above (pp. 97, 98) this process was interpreted as a mechanically disturbed fusion of the blastoporus edges. According to general theory (pp. 49, 50) this process should be incomplete in the median anterior and posterior parts of the germinal disc edge, leaving open the

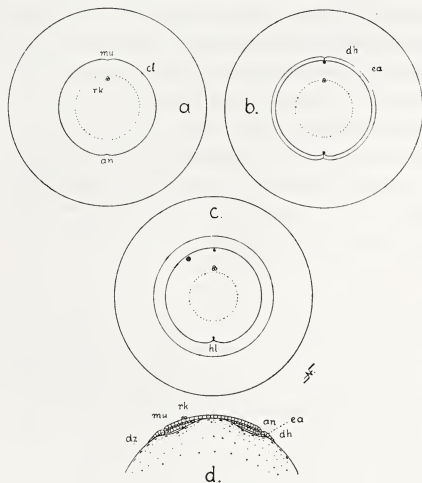
mouth and the anus. This can be easily imagined when comparing Textfigures 31 and 32 with a different interpretation: In a yolky coelomate, in which (starting from something like Textfig. 6) secondary conditions as shown in Textfig. 32b 1 were achieved, the median section should show a situation as in Textfigure 32b; the anterior and posterior parts of the blastoporus lip would continue to provide the upper limit of the mouth and the anus (as in Textfig. 6f, g). Only the lateral edges of the blastoporus would approach each other on the lower yolk face. This view also can be applied to ⁹⁹ Textfigures 32c and 31f; one would simply have to add those parts of the germ layers that unite below the mouth and the anus.

In cephalopods it is easy to identify the positions at which the mouth and the anus should be formed following the general morphogenetic type of the coelomates or the special molluscan type, namely the most anterior and posterior medial edges of the newly multilayered germinal disc. Sometimes these points (cf. e.g. Pl. 1, Figs. 11-12) are more or less clearly marked, at least for a short period of time; but a distinct establishment of the anlagen of mouth and anus (Pl. 2, Fig. 4) occurs only later, at a time when the epibolic growth across the yolk mass is very advanced so that the actual blastoporus edges are no longer so directly identifiable.

The same picture appears in a medial section of a germinal disc like that shown in Textfigure 31 g, i.e. no trace of mouth and anus once the blastoporus edge has become 'dissolved' at the yolk surface. But all these pictures can be interpreted by comparison with the diagram of Textfigure 33d, so that one may assume that in cephalopods the mouth is derived from an anterior, transiently closed blastoporus remnant—in a way similar to the formation of the anus (from a posterior remnant) in other molluscs and in annelids (compare Textfig. 7g with 6g). Subsequent development shows both as if they were following exactly the morphogenetic plan suggested by the present diagrams, i.e. as if the anlagen had been established according to the pattern of Textfig. 33, but then had been rapidly closed, along with the continuing unification of the germ layers. These pictures provide an interpretation of the actually observed patterns in an attempt to bridge the gap reflecting the contrast between the cephalopod pattern and the normal molluscan and coelomate development.

The epibolic envelopment of the yolk organ by the germ layers (Textfig. 31 g, Pls. 2, 14, 32) places the greater part of the yolk organ in the outer "yolk sac". This envelopment is achieved by a particular formation that is derived from the blastoporus edge and becomes distinct from the anlage of the embryo proper (Pl. 14, Fig. 4 ea), name-

ly the "yolk envelope". This envelope overlies the yolk cells, which in turn form the "yolk epithelium" enveloping the entire nutritive yolk; the yolk sac envelope consists



Textfigure 33. — Diagrams illustrating formation of the mouth, anus and yolk envelope in cephalopods. (See also Pl. 1, Figs. 10-12). 25× natural size. Whole eggs with germinal discs.

a) Germinal disc with ring-shaped peripheral thickening and sharply limited contour. The yolk cells reaching beyond the contour are not shown. rk: polar bodies, situated in the anterior part of the medial line; cl: limit of the central gap, i.e. the central limit of the mesendoderm (cf. Textfig. 31f). In this central part of the germinal disc, the endoderm is represented by the yolk organ, which here lies immediately below the ectoderm, thus completing the inner germ layer; mu: position of the mouth; an: position of the anus, marked as an indentation in the blastopore edge (which is still identical with the edge of the germinal disc). According to general theory (Bütschli, 1877), the foremost part of the blastopore edge should form the mouth, the rearmost the anus; in cephalopods they in fact are formed by the corresponding parts of the germinal disc, as illustrated by the following diagrams:

b) Starting from the ectoderm of the blastopore edge, which will be caught up by the mesenchyme, the yolk envelope forms as the outermost layer of the prospective outer yolk sac. It takes up the entire periphery of the germinal disc, which raises a special problem: at the end of embryonic development, the connection between the yolk envelope and the body of the embryo is limited to a small distance below (behind) the mouth; the anus lies far away from it. From stage II onward, the rim of the germinal disc comes in two parts as it were; one is the rim of the yolk envelope (derived from the ectoderm, excluding the endoderm), the other is the rim of the embryonic body (ea), which is here limited by a solid line. The mesendoderm is limited to this anlage of the embryo proper. The sites of the mouth and the anus (which are not yet visibly differentiated) are overtaken by the yolk envelope. The figure thus visualises an archetypal situation, to which the pattern actually observed can be related.

c) The respective positions of the mouth and the anus are slightly shifted inside the anlage of the embryo proper; the anal site forms an indentation (Pl. 1, Fig. 12), the so-called "posterior gap". The central gap is decreasing in size, while the yolk envelope continues to cover the yolk organ.

d) Medial section through the stage represented by c, with the assumed archetypal positions of the mouth and the anus: a small part of the blastopore lip has become bent inwards, thus limiting two orifices. These in fact appear only later (by secondary junctions of ectoderm and endoderm), but in the corresponding positions, as will be shown below. Dz: yolk cells, i.e. nuclei of the yolk organ (yolk epithelium). The limit between the embryo proper (ea) and the yolk envelope is not distinct immediately.

of a thin ectoderm layer advancing virtually simultaneously (like a girth surrounding the yolk mass) and a mesenchyme layer that lags behind slightly; within the latter sinus-like blood spaces will develop later.

The yolk envelope has to be viewed as a special embryonic organ, more precisely as a differentiation of the blastoporus lip which has become necessary due to the increase of the yolk volume, which must have occurred in the course of phylogenesis. In proportion to the incipient inhibition of a blastoporus seam formation, the progressive differentiation of the yolk envelope provided a compensation.

The *endoderm* shows a peculiar reaction to the developmental obstacle formed by the yolk organ: Instead of enfolding it by epibolic growth, as would correspond to normal organogenesis (Textfig. 32 b), the wound is closed by slow forward (downward) extrusion of the yolk organ, the gut anlage becoming progressively constricted (cf. Textfig. 50). In phylogenetic terms this novelty cannot have been achieved in one single step; one has to assume an intermediary stage in which the endoderm rudiment enclosed part of the yolk organ, whereas the remaining part became extruded by the gut constriction (cf. Textfig. 32 cl). In any case this was a process comparable to a restitution of normal conditions after perturbation by an adverse factor (the yolk). This restitution has been incorporated in the typical development.—Thus the yolk sac is not just a hernia-like sac in an ‘overfed’ embryo.

A critical remark has to be added here: According to the earlier authors (see in Korschelt and Heider 1893) the yolk cells disperse early on to the yolk surface; this statement is erroneous. In fact once the circle of “blastocoelons” surrounding the blastodisc disappears, this is not due to dispersal leading directly to the epibolic yolk enfoldment but to the retraction of the rays under the edge of the germinal disc (Pls. 1 and 13). The yolk enclosure is essentially due to the yolk envelope; beneath it the yolk epithelium does follow in that the increasing number of dividing yolk cells progressively replaces the thin plasmic pellicle by a syncytial layer.

A clarification is also needed regarding mesoderm development: In cephalopods as in any mollusc or coelomate, the mesenchyme and the mesoblast have to be distinguished. These two elements are not easily distinguished even in the more typical molluscan ontogeneses, and probably there has been confusion between them in the past; in cephalopods I have not been able to distinguish their respective elements after their separation from the blastoderm or the primary germ layers, nor to follow their respective fates before an advanced stage of organogenesis allowing one to recognize individual

organ anlagen and their components. I have not seen the special differentiation of "mesoderm" from the ectoderm described by Teichmann (1903, pp. 47onward), no more than the "gonad anlage" described by him.

It has already been said (pp. 97, 98) that a clear-cut separation of the mesoblast from the endoderm is not recognizable. But I hope to be able to elucidate this distinction to a certain extent in *Octopus* and in *Argonauta*, since their endoderm formation shows conditions more intelligible according to Textfigure 31 than what is seen in decapods in that an epithelial connection with the blastoderm appears partly conserved. For the moment we have to content ourselves with the collective term mesendoderm, which includes a mesenchyme of ectodermal origin along with a mesoblast belonging to the primary endoderm. The mesoblast should give rise to the entire coelomic system, although such a derivation cannot be demonstrated for lack of distinctive features (Naef 1905*). The elements of the coelomic system, like those of blood vessel walls, the connective tissue or the musculature, appear to differentiate *in situ* from an originally homogeneous, parenchymatic cell material lying between the ectoderm and the subsequently distinct epithelial endoderm, in an arrangement already corresponding well to the anatomy of more advanced embryonic stages.

A more detailed, special description of these processes will be given later in the context of organogenesis dealing with the gut, the coelomic and circulatory systems.

4th Period: Mesoderm Grouping in Preparation of Outer Organ Anlagen

Germ layer formation and subsequent processes have produced a germinal disc, the typical form of which is shown in Plate 2, Figure 1: Three zones can be distinguished: 1) a thin, single-layered marginal zone (dtz), which is the yolk envelope under which the yolk epithelium has been retracted almost completely, 2) a ring-shaped, multilayered zone appearing light-shaded in the preparations (vr) below which the mesendoderm is situated. (From now on we will mention only the mesoderm, since the endoderm, which lies directly on the yolk and is newly segregated, newly constituted or derived directly

* Scientific Editor: it is not clear whether 1905 is a typing error (1909 being meant) or whether it refers to an early, unpublished study not mentioned in the reference list.

from the marginal part of the blastoderm, is of no essential importance in the surface aspect.) 3) A central (apart from the yolk epithelium) single-layered zone called the central gap (cl) since in this zone the endomesoderm is closed by the yolk organ only (Textfig. 31 g). The outer limit of zone 2 (vr) comprises the body of the embryo proper, i.e. the anlage of the cephalopod body excluding the yolk sac. Posteriorly (below) it has a notch (hb), which corresponds to the location of the anus and which can be derived from the above-mentioned (p. 97) gap in the endoderm ring (Pl. 1).

The mesodermal mass does not yet show any further differentiation visible from the outside, but it soon takes on increasing importance with the spreading of the germinal disc that soon forms a cap covering the yolk while the central gap disappears. Concentrations of mesoderm cells become visible under the ectoderm; with the technique used (explanation for Pl. 1) these cell groups appear as lighter, ill-defined patches against a darker background. (In lateral view the germinal complex still appears flat under the dissecting microscope.) These patches become increasingly distinct and can, by comparison with later stages, be partly identified as the anlagen of certain organs:

The outermost marginal zone of the embryonic body (Pl. 25, Figs. 2-4) thus corresponds to the arm crown; a broad zone lying inside the upper semicircle is the anlage of the embryonic head, on which the eye rudiments soon become visible as transverse oval rings (Pl. 2, Figs. 3-5). In the central part, the anlage of the muscular mantle 103 forms a light ring surrounding the central gap (or the patch corresponding to the shell epithelium). There is only a positional correspondence, perhaps a relationship in terms of developmental mechanics, but no identity. The shell epithelium becomes distinct at about the time when the central gap disappears due to mesenchyme spreading in this area. (See Pl. 2, Fig. 4 where the central gap 'is still visible inside the contour of the shell epithelium').

The light patches lying on either side of the posterior (lower) part of the mantle rudiment can be interpreted as the anlagen of the gills; between them in the midline one finds a light streak in a position that will later be taken by the anal papilla and the hindgut. This is the site in *Loligo* where one can see the small epithelial plate, which was considered the anlage of the midgut by Korschelt (1892) and Teichmann (1903), but which in fact is much more extended.

Thus the mesoderm concentrations give the germinal disc a typical architecture long before any anlagen become distinct in the untreated embryo or in its surface structures; this structuring can indeed be more detailed (Pl. 15, Fig. 1): From the pos-

terior end of the semicircular head anlage the statocysts separate as small, hazy patches; the arm crown is subdivided into portions corresponding to the individual arms. It is surprising that a cell concentration similar to an arm rudiment appears in the mid-line between the anlagen of the ventral arms; it was regularly observed in loliginids, sepiids, sepiolids, oegopsids, polypodids [octopodids], argonautids, i.e. in all the groups that I was able to investigate for their embryology (see figures in Pls. 2, 23, 26). This can only be a rudimentary arm anlage, for while the arms develop the light patch disappears; in any case the formation is part of the arm crown. Since the number of arms in decapods is an undoubtedly reduced one, the occurrence of such rudiments is not surprising.

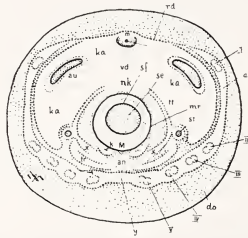
However, we have to think of certain shifts that have taken place in this marginal zone of the embryonic body (cf. pp. 100-103): Whereas originally (Pl. 1, Fig. 10) the germinal disc was virtually circular in outline, it became posteriorly indented in subsequent stages, in the course of the differentiation of the marginal parts; this posterior indentation (Pl. 2, Fig. 1 hb) marks the site of the anus (Cf. Pl. 14, Fig. 4 hl; Pl. 25, Fig. 1 ml). The resulting shift of elements (of the bauplan) removes the prospective anus from the edge of the germinal disc, which leads to the unification of the parts formerly adjacent to the gap (Pl. 2, Fig. 4). The relationship may be inverted, however, 104 meaning that the edge of the germinal disc representing the arm crown (in other words, the molluscan foot anlage) becomes separated from the anal anlage and closes the ring at a place whose prospective position (the anus still marking the morphological hind end) is below and in front of the anus. This means also that the connection between the yolk envelope and the embryo proper is restricted anteriorly to a zone situated between the arms and thus follows the latter in any shifting.

The process can be interpreted on the background of protomolluscan and molluscan history (p. 69) as follows:

Whereas the creeping sole, i.e. the phylogenetic "anlage" of the foot, reached to the anus in the annelid and premolluscan type, this connection became dissolved later on. The morphological hind end rose above the posterior end of the developing foot (Textfig. 10 c), and they became progressively independent from one another. Thus the medial element in the earliest, still indistinct arm crown anlage (Cf. Pl. 2, Fig. 4 hb, Fig. 5 x) probably represents the posterior end of the newly independent (in relation to the anus) molluscan foot; in cephalopods it remains rudimentary while other parts continue their differentiation. Note also the primary uniformity of the arm crown anlage which undergoes subdivision only later. (Cf. Textfig. 17 h, g, b)

At the stage shown in Plate 2, Fig. 4, the rudiments of the mantle, the anus and the gills still lie in a (darker) zone which corresponds to the visceral sac of a developing conchiferan. This zone becomes more distinct at the following stage (Figure 5), being surrounded by a low rampart, on either side of which the statocysts are situated in the darker zone. At the dorsal midpoint this rampart is interrupted by a gap (nk) which corresponds to the future nuchal attachment. The parts of the rampart lying above (anterior to) the statocysts provide the anlagen of the funnel pouches, the lower (posterior) parts—in contrast to what could be expected—do not give rise to the funnel tube rudiments; the latter belong to the cephalopodium and are differentiated independently from the funnel pouch. The rudiment marked “waistband” (gb) does not give rise to any externally visible organ; its position corresponds to the place where the funnel gland will develop later. Topographically it corresponds to the domain of the parietal strands of amphineurans; their lateral parts contain the anlagen of the so-called visceral ganglia, which should be named more properly the pleural ganglia.

The funnel tube rudiments appear strikingly late as rather indistinct structures (Textfig. 34 tr): In Figure 5 of Plate 2 there are hazy lines pointing from the statocysts (st) to the ventral arms (V), from which they are not always separated (Pl. 15, Fig. 1).



Textfigure 34. — Germinal disc of *Sepia officinalis* at the beginning of folding processes. 10X natural size. — rd: limit of the embryo proper; I-V: arm rudiments of the right side; ak: connecting cell complexes of the arm crown; do: yolk sac; y: position of the medial rudiment in the arm crown; an: anus; M: muscular mantle; k: gill; x: waistband (position of the pleural part of the perioesophageal ring); tr: funnel tube rudiment; ka: head rudiment; au: eye; vd: fore gut; m: mouth (with unlabeled rudiment of the poison gland); nk: position of the nuchal attachment; sf: shell fold; se: shell epithelium; tt: funnel pouch; mr: mantle rim; st: statocyst.

This figure illustrates the primary shape and arrangement of rudiments when the germinal disc is stretched out due to the extreme yolkeness of the egg. With decreasing yolk content, this extension (which is opposite to the prospective topography) would partly disappear, leading to a situation similar to that shown in Plate 8, Figures 1-4. The respective shapes of the rudiments there are almost the same, but they are arranged in a much more normal pattern from the outset of their differentiation.

From this situation I draw the conclusion that the funnel tube is a relatively recent
105 neof ormation of the cephalopods, which is derived from the more ancient arm complex.

All these processes are not easily observed and described in detail, but they are sufficiently distinct to be recognized for their morphological significance. During this phase of development the yolk envelope encloses about one-half of the yolk, sometimes a little less (*Sepia*), often a little more (*Octopus*, *Loligo*; cf. Pls. 8, 9, 32). The overall effect is that the cell material forming the embryo proper is situated in its definitive position when the folding processes start that will shape the externally visible organ complexes and will give the embryo its morphological imprint in relief-like clarity (Pls. 2 and 15).

This folding process is comprehensible only with the background of the above description, as the result of a combination of already ordered and directed formative forces.

5th Period: Folding Processes in the Embryo and the Establishment of Surface Architecture

The typical layout and arrangement of outer parts is visible best in Plates 2 and 15: The arm crown now is a flat ring surrounding the embryo proper and forming its limit against the yolk envelope. This ring is open above (anteriorly) in the area of the
106 mouth. In the ring-shaped rempart, the 8–10 individual arms form second order elevations, each of which consists of two distinct papillae. This feature (Pl. 15 and 23) is observable at least in the largest, particularly well-structured embryos.

The significance of this bipartite structure is not clear to me. It is not very likely that two original arm rudiments have become united, which would partly explain a reduction of the arm number from a tetrabranchiate state (*Nautilus*) to the dibranchiate condition. It is more likely that the phenomenon is related to a much earlier process in the history of the class. In teuthoids and octopods this feature is barely or not at all expressed.

In decapods, 4 arm rudiments lie on each side in the lower part of the embryo; only one, the future dorsal arm pair lies in the upper part, strikingly far removed from

the others, not far from the mouth. To understand this positional relationship in the embryo and integrate it topographically into the adult organization and the typical architecture of other molluscs, one has to remember the contents of Textfigures 20 and 31, namely the fact that the yolk mass has very strongly distended the area of the blastoporus and of the prospective mouth, resulting in an overall flattening of the embryo; thus the marginal parts of the blastoporus lie at the periphery of a flat or more or less cap-shaped germinal disc. Remembering that the parts of the germinal disc that lie outside the arm crown represent only the envelope of the yolk sac, we must consider the primary position of the arms as adjacent to the blastoporus; thus mere distance relations among individual arms cannot be of great importance. Nevertheless, the dorsal arm rudiments are not united, since between them lies the mouth which can be considered homologous to the uppermost (anteriormost) part of the blastoporus (pp. 100, 102). Thus they still hold a position in relation to the mouth comparable to the position which the rear end of the foot anlage had in relation to the anus, and which it gave up only later (pp. 104, 105); in other words, anteriorly the cephalopodan foot still reaches to the mouth, and the latter here closes the circle.

The mouth anlage lies in the domain of the slight semicircular elevation already identified as the anlage of the head as much as it lies at the periphery of the embryonic anlage (Pl. 2, Fig. 6). It has lost the direct connection with the endoderm, so that one cannot speak of an immediate transition from the blastoporus to the mouth as in other molluscs. It forms a transverse oval, epithelial depression with a prominent rim, the lower, more sharply incisive part forming the anlage of a stomodaeum.

On the lateral parts of the head anlage one finds the prominent, slanting oval eye rudiments (Pl. 15). They are (Fig. 1) slightly bulging epithelial thickenings (retinal anlagen) surrounded each by a marginal fold that rapidly develops into a closing membrane covering the retinal thickening. Behind the eyes and towards the midline of the embryo a conspicuous thickening is recognizable as the result of an epithelial proliferation. Medially it gives rise to the cerebral ganglia, towards the eye it forms the optic ganglia, the rest being prospective white body. These formations are not only a topographically connected complex, but also a morphological unit, the elements of which cannot be clearly separated from one another at these early—as well as at much later—stages. The white body in particular cannot be clearly distinguished from the cerebral and optic ganglia for a long time; it remains closely connected with them and shows a strikingly homogeneous histological aspect similar to the structure of the ganglia.

I should therefore like to suggest that the white body is an endocrine gland derived from the central nervous system rather than a blood gland as generally inferred. This hypothesis will have to be tested by future anatomical and physiological investigations.

Proceeding from the eyes to the mantle anlage we encounter the funnel pouch rudiments (Textfig. 34 tt). They are rib-like elevations reaching posteriorly and laterally to the pit-like statocysts; anteriorly they have ill-defined, blind ends. The medial epithelial zone will form the "nuchal attachment", but this differentiation will take place much later, the funnel pouches then becoming connected directly with this attachment. The latter apparently is a phylogenetically younger part, whereas the funnel parts probably represent a very ancient conchiferan organ. The funnel pouch anlagen are now connected directly with the statocyst rudiments (Pl. 15, Fig. 2), which first appear as round discs of modified epithelium with cup-like elevation of the rim. On their medial sides they grade into the low elevation of the "waistband" (p. 105) which appears to form a morphological unit with the funnel pouches. In surface aspect it represents an ill-defined transverse band in approximate continuation of the funnel pouches; it is still more conspicuous than the funnel tube rudiments. The latter lie more ventrally and still present no marked elevation. In contrast, the gill rudiments lying above them have become distinct papillae embracing the mantle rudiment laterally and upwards, thus providing a first hint of the future gill attachments; between them an inconspicuous elevation marks the anlage of the anal papilla.

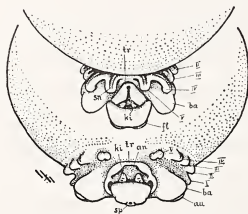
108 The anlage of the muscular mantle now forms an elevated, broad ring, the outer rim of which represents the future mantle edge, whereas the inner rim is the anlage of the shell fold. Between the inner and the outer rim lies a shallow, gutter-shaped depression. The shell fold surrounds the slightly lowered shell epithelium and thus forms the anlage of the shell sac. It should be emphasized that the anlage of the muscular mantle is connected with the margin of the shell epithelium and shell sac, which corresponds topographically entirely to the (not yet formed) shell. It thus appears as the homolog of the primary mantle *margin*, as suggested earlier (Cf. Vol. 1, p. 93; and above, Textfig. 22 b).

The differences in surface levels now appearing are rapidly increasing, both in individual parts and in the whole embryo. The latter cannot be termed a germinal disc any longer. It forms a cap-like, though still-thin cover that surrounds the greater part of the egg. With increasingly distinct relief structures this cap raises above the yolk

level, due to constrictions, especially in the arm crown which contracts like a rubber band, so that the differentiation between embryo proper and yolk sac becomes very distinct. The ring formed by the mouth and the arm crown, which has 'taken' the position of the blastoporus (pp. 101, 103), thus becomes constricted in a way suggesting a further restitution of normal positional relationships previously disturbed by the yolk plug (p. 99). Given the conditions already mentioned, this does not mean a mere restitution of primary morphological relations, as will be shown again below.

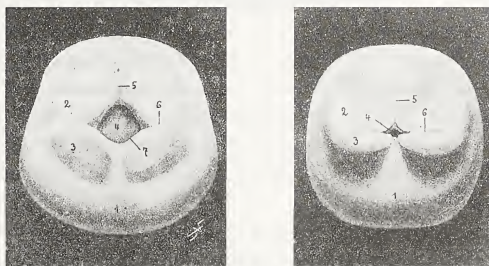
In the course of this process, which modifies the overall aspect of the embryo, similar modifications of detail in the various parts occur, as can be seen in Plates 4 and 17.

109 The mantle anlage, especially its outer wall, rises and grows into a thick fold that surrounds a slit-like, circular mantle cavity which becomes rapidly deeper in the ventral part. Thus the gills and the anal papilla become covered and rapidly disappear due to an invagination-like process (Textfigs. 35). Meanwhile the shell fold contracts and closes the shell sac, inside which (below the cover) the shell will be formed later. The final contraction of this shell fold gives the impression of a fusion (Textfig. 36 and 37) of the edge along three seams, one anterior and two lateral ones. Thus an inverted T pattern is formed (Cf. Pl. 2, Fig. 11), the meeting point of the three limbs containing the rest of the shell fold. These seams mark the anlage of Hoyle's organ (Pl. 16, Fig. 2), which will be conserved to the hatching stage. (I suppose that this organ serves as dual function, the mucous glands protecting the posterior end and assisting in capsule perforation at hatching, the latter process being further enhanced by a small spine in the sepiolids 'Pl. 23'.)



Textfigure 35. — Progressive folding of parts of the embryo in *Sepia officinalis*. 10× natural size. — tr: funnel tube; sn: sucker rudiments; ki: gills; I-V: arm rudiments; ba: cheek humps; fl: fins; an: anus; sp: shell sac pore; au: eye. — Orientation of the embryo: head up, as in all the advanced stages figured in the Plates. Ventral view.

While the shell fold contracts and thus hints at a shell enclosure (although the shell is not yet formed) (Cf. Text figs. 36, 37), the fin rudiments appear on the outside
 110 of the shell fold as its secondary derivatives (Pl. 2, 15). They begin as low elevations formed by mesoderm concentrations embracing the lateral branches of Hoyle's organ (wherever these are visible, in any event on each side close to the shell sac pore). Once they have a distinct form as round papillae or lobules, the last opening of the shell sac always lies medially between them. This originally close relationship with the shell sac is important for the phylogenetic derivation of the fins, but also in the context of their subsequent development, especially for the morphological comprehension of their articulated connection with the underlying parts (Vol. 1, pp. 95, 114).



Textfigures 36 and 37. — Two stages (IX and X) of the mantle sac rudiment in *Sepia officinalis*, in caudal view. 35× natural size (cf. Pl. 15).

1: muscular mantle; 2: dorsal part of fin rudiment; 3: ventral part of fin rudiment; 4: shell sac pore, closing in an inverted T-shaped seam; 5: gutter-shaped medial continuation of the latter; 6: gutter-shaped lateral continuations, marking the prospective branches of Hoyle's organ; 7: edge of shell fold.

Note the positional relationships of the fin rudiment (in Textfigure 37) with the shell sac pore (4), a ventral portion (3) becoming very distinct (See also Plate 23).

One special point has to be emphasized: The fin rudiments are not dorsal, longitudinal folds of the integument that could be derived phylogenetically from correspondingly orientated stabilizer brims of a powerful swimmer—in contrast to what the modern decapod types (in which they are most strongly developed) would suggest. Their primary orientation is more or less perpendicular to the longitudinal axis of the swimming animal (p. 73), a situation emphasized by the importance of the component lying ventrally to the shell pore. The transverse seam (6 in Textfigs. 36, 37) which

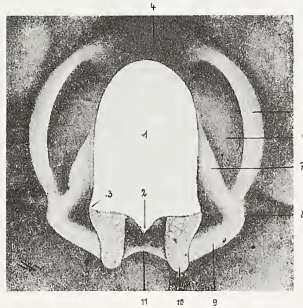
starts at the pore does not originally lie at the posterior edge of the fin as derived conditions (Pls. 7, 8, 23) would seem to suggest; the seam or the resulting lateral branch of Hoyle's organ lies on the upper *surface* of the fin. But in most recent decapod types the posterior part of the fins degenerates so that the posterior end of the fins gets its clearly terminal position; in sepiids (Pl. 27) this state is attained through an overall modification. The primary and typical condition is a strong ventral extension of the fins, in other words, a more or less transverse position rather than a longitudinal orientation, at least in juvenile forms. (Cf. Textfigs. 44, 55, 71, 74, 79, 85, 87; also vol. 1, p. 516)

The corners of the funnel pouches appearing on each side of the mantle rise up to become bowl-shaped; by the subsequent contraction of the embryo and the longitudinal growth of the mantle they finally come to lie inside the mantle (Textfig. 35) thus taking their functional position (Cf. Pls. 17, 28, 34). The statocysts close down as pit-shaped formations, remaining in communication with the outside by a fine pore (Pl. 3, Fig. 8; Pl. 26, Fig. 8) which will finally be totally contracted. Inside a blind-ending canal starting from the statocyst is conserved as a remainder of the primary connection with the ectoderm; it can be viewed as an analog of the Ductus endolymphaticus of the vertebrates.

The funnel tube rudiments now rise up rapidly (Pl. 15, 27) to form a distinct transverse fold, the lateral parts of which are particularly elevated (Textfig. 35); they extend upwards and laterally to join the funnel pouches, thus achieving the unity of the funnel apparatus (which thus appears as a genetically secondary unity). The two lobes of the funnel tube then unite to form a tube (Pls. 4, 9, 17, 27, 35) in which the low connecting medial part of the original funnel fold also participates. Elevations appearing at the points of fusion between funnel tube and funnel pouches continue to rise towards the deeper parts of the mantle cavity; these are the funnel retractor rudiments.

At first sight it may be surprising (Textfig. 32) that the outer funnel tube opening is not left open when the "funnel lobes" become fused to form the tube—as might be expected (if one could view anlagen as the simple recapitulation of phylogenetically older conditions).

The outer opening becomes indeed closed; but the closing part is not a continuation of the seam of fusion to the funnel tube end, it is made of special parts: The "sharp edge" of the connecting medial part of the funnel fold closes on itself (instead of forming the opening) and thus forms a narrow 'window' closed by a thin plasmic

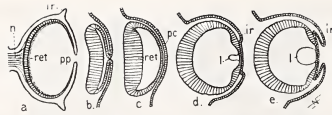


Textfigure 38. — Anlage of the funnel complex in *Sepia officinalis* (cf. Pl. 15, Figs. 4 and 5). The mantle sac (shown in Textfig. 37, the same orientation) is cut off at 1, so that the mantle cavity is exposed. 2: ridge connecting the visceral complex with the mantle, representing the rudiment of the mantle septum containing the cell material of the prospective Arteria pallialis medialis; 3: position from which the lateral edge of the gill rudiment becomes connected to the muscular mantle; 4: position of the prospective nuchal attachment; 5: outer wall of the bowl-shaped funnel pouch; 6: cavity of the latter; 7: funnel retractor reaching to the middle piece of the body, but not yet extending to the muscular mantle (cf. *Nautilus*: Vol. 1, p. 68, and above. Textfig. 25); 8: funnel edge corner; 9: one half of funnel tube; 10: gill with rudiments of gill lamellae; 11: position of prospective funnel opening.

pellicle rather than by a double epithelial cover, not to speak of any embryonic muscular tissue similar to other parts of the funnel tube. This process appears like gluing together the feeble marginal parts of a "virtual" opening that are torn open later on; however, the material used in this process is morphologically distinct. The closing membrane should thus be considered an embryonic organ as defined in the Introduction (p. 23).

The eyes become closed by the continuous contraction of the ocular folds and then form slightly elevated blisters; they are externally distinct but show no further structuring (Textfig. 39 c, Pls. 3, 15, 33); subsequently the closing membrane will form, starting from the site of the closed pore, the inner lens rudiment; the complementary outer segment will be formed much later. Around its periphery a ring-shaped elevation appears, the iris fold anlage (Textfig. 39 d, Pls. 4, 16, 34). Thus the latter belongs to (the most prominent part of) the eye ball itself, in contrast to the so-called corneal fold (see further below).

In general terms the head anlage shows an increasingly distinct architecture; so one is tempted to see the origin of this architecture in the appearance of various organ



Textfigure 39. — Diagrammatic frontal sections of the right eye in different cephalopods.

a) *Nautilus*. b-e) embryos of *Sepia officinalis*. n: Nervus opticus; ir: iris fold; pp: primary pupil; ret: retina; pc: primary cornea; l: lens. — The flattening of the inner part in b and c is due to the presence of the yolk mass, on which the embryo is stretched out as a relatively thin layer; this flattening has no phylogenetic significance (in the sense that originally the functional retina would have been a flattened structure).

Apart from this special aspect (flattening), the stages figured can be interpreted as a recapitulation of more or less completely corresponding stages of an ancestral series, which have attained their respective functional stage directly (rather than undergoing further bauplan modifications). This is perfectly conceivable since in different extant cephalopods the juvenile eyes become functional at different levels of architectural complexity (from the last stage figured above, as far as I can say from my own observations; cf. Pl. 8, Figs. 7 and 8). This problem will be discussed in detail elsewhere.

rudiments. See for example Plate 2, Figure 12 Note here the darker fields lying medially and posteriorly from the eyes:

These fields mark the position of the optic ganglia underneath. More medially, separated by a light stripe in the midline, lie the cerebral ganglia; more anteriorly the anlage of the buccal mass. The slightly bulging cushions, which are separated by furrows, are parts of the future white body (Cf. p. 108); they are so strongly contracted now that the eye ball appears to be carried by a thick, massive stalk, the center of which is occupied by the optic ganglion.

- 113 One has to imagine that a lesser extent of these organ rudiments (the ganglion itself is still small) would make these stalks thinner, so that their rudimentary state would be reminiscent of what *Nautilus* shows us, i.e. globular, thin-stalked, vesicular eyes. See also Textfigure 41 for a morpho-physiological comparison and phylogenetic interpretation.

The oval invagination, which we have recognized as the mouth anlage, also shows some modifications: Somewhat before its center (Pl. 20, Fig. 6, gd; Pl. 8, Fig. 2; Pl. 15, Fig. 3; Pl. 23, Fig. 1; Pl. 26, Fig. 7) a small secondary depression appears; it is soon shifted posteriorly and represents the unpaired anlage of the "salivary glands", the large venom glands. This anlage soon disappears from the surface aspect, because the stomodaeum grows deeper and the upper edge of the mouth is drawn forward.

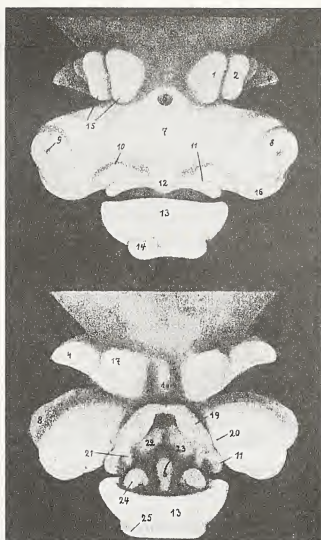
As mentioned earlier the arm rudiments come to lie closer together, due to the constriction of the yolk, and in the apical view used up to now (Pl. 15, Fig. 5) they are then hidden by the embryo. When viewing the embryo from the dorsal side (Pl. 2, Fig.

12), long papillae-shaped dorsal arm rudiments appear, 3 on each side in decapods, 2 in octopods; a ventral view shows 2 ventral arm rudiments on each side in both cases (Pl. 4). The distance separating the first and second arm pairs so distinctly at earlier stages (p. 106) has now disappeared; the first arms are still separated from one another by the mouth
 114 anlage joining it increasingly closely from each side (Textfig. 40).

The bipartite structure of the arm rudiments (wherever distinct at earlier stages, cf. p. 107) has virtually disappeared, except for a fine groove on the inner and outer surface of each arm rudiment (Pl. 28, Fig. 5). The first indications of sucker rudiments are recognizable in the inner groove (Pl. 21, Fig. 4).

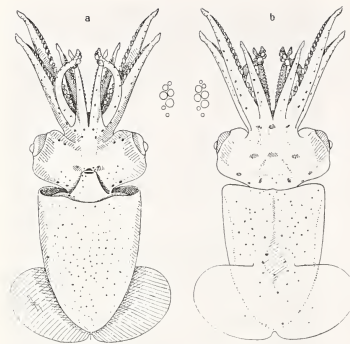
The arrangement of the arms becomes particularly clear in lateral view (Textfig. 44 and Pls. 6, 27, 33). It now appears that the positional relationships of the parts have been thoroughly modified in a direction towards definitive organization (Cf. p. 105); The three dorsal arm pairs (in decapods), the outer two of which (Pl. 2, Fig. 7; Pl. 15, Figs. 1 and 6, marked II and III) were situated much more ventrally (close to the statocysts, see Textfig. 34) at earlier stages, are now beginning to take their definitive dorsal position relative to the eye, thus moving away from the statocysts. This is an enormous shift in primary correlations, the extent of which can be seen best in the embryos formed from large eggs, as in *Sepia*, *Sepiolo* and *Loligo*.

This development again requires a phylogenetic interpretation; there is indeed no other reason than a likely dependence on earlier conditions to explain why the arms



Textfigure 40. — Embryos of *Loligo vulgaris*, stage XI, in dorsal and ventral view. 44× natural size.

1-4: arm rudiments, 5: yolk sac; 6: mouth; 7: position of cerebral commissure; 8: eye ball; 9: position of lens rudiment, surrounded by iris fold rudiment; 10: part of the white body; 11: funnel pouch; 12: position of nuchal attachment; 13: mantle sac; 14: fin; 15: rudiments of arm pillars; 16: cheek humps; 17: ventral arm; 18: funnel opening; 19: funnel lobes; 20: scar of statocyst closure; 21: funnel retractor; 22: pleurovisceral ganglion; 23: anus; 24: gill; 25: fin.



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Textfigure 41. — Juvenile *Octopodoteuthis sicula* from the plankton in the Naples area (Vol. 1, p. 337). 4X natural size.

This figure illustrates the general topography of typical embryos as shown in Textfigure 40, especially with regard to the ocular stalks, which can show very similar shapes at postembryonic stages. It is possible to consider the general form of the embryo as a reminiscence of an earlier condition achieved in the course of phylogeny, of course not directly as an adult stage, but as a juvenile condition not too far removed from the adult state.

only the beginning and the end being omitted. Note especially the conduct of arm rudiment III, which has just passed the statocyst in Fig. 1, whereas in Fig. 7 it is already situated above in front of the eye. See also Plate 6, Figures 1-3.

Since the visceral sac is sharply delimited by the ring of the waistband and funnel pouch anlagen (Pl. 3, Fig. 1; gb and tt), it is easy to see its increasing independence from the arm crown, the latter being situated further and further away, before (under) the head, while the funnel tube retains an intermediate position.

This rearrangement is also indicated by the yolk envelope or the outer yolk sac as a whole. In morphological terms, the early outer yolk sac apparently corresponds to the entire medial part of the ventral side, from the mouth to the anus. The midline is forced open (into a circular line) by the enormous yolk mass (Textfig. 33 c) and thus

are not formed in their definitive relation to other parts of the head. To understand the whole process, we have to start from the statements and interpretations presented earlier (pp. 104, 105). What is happening here is a likely continuation of the same developmental tendency, which can now be better verified since the arm rudiments characterize unequivocally certain parts of the foot: the whole arm crown modifies its positional relationships to the head by moving away from the visceral sac, the distance between the arms and the anus becoming ever greater in that the arms approach the mouth, a movement that looks almost like a migration of individual arms.

The primary affinity of the arm crown to the morphological hind end is completely lost by this process, whereas the arms gain a new, highly significant relation to the eyes. Most of the process can be seen in Figures 1, 4 and 7 of Plate 3,

surrounds the dorsal side. The incipient yolk sac thus occupies at least the medial part of the sole of a chiton's foot, i.e. of its muscular mass. This primary positional relationship is then thoroughly modified, as illustrated by Plate 26: Figure 1 still shows a virtually undisturbed initial condition. If we turn it upside down (yolk sac down), the arm crown aligned horizontally, the topographical conditions are easily comparable to the diagram of Textfigure 17 g; just remember that the cephalic organs are extremely large at early stages (as in vertebrate embryos) whereas the vegetative, more simply structured parts of the visceral mass are much smaller. Following the changes in a lateral view (with identical orientation) from Plate 26 through Plates 27, 28, 29, we find a stepwise modification of the relation between the yolk sac and the embryonic body with the arm crown, resulting in an extreme reduction of the yolk sac, which becomes a small appendage lying below (behind) the mouth, whereas the arm crown contracts in very close vicinity to the mouth.

Whereas the earliest stages of these modifications of the primary bauplan shed light on the phylogeny of molluscs in general (p. 104), the shifts described here have to do with the conchiferan phylogeny, and with the separation of the cephalopodium from the visceral sac, i.e. the process illustrated phylogenetically by the juxtaposition of Textfigures 17 h, g and b—although the particular architecture of the cephalopodium already foreshadows, at least partly, the general cephalopodan features and the special dibranchiate characters. Of course the bauplan of primitive conchiferan embryos can be recapitulated only in parts that are still existing.

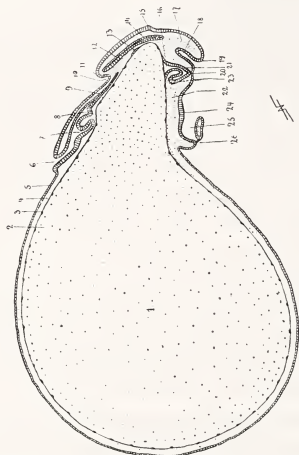
Put simply: The ontogenetic shifts in cephalopods argue in favour of a derivation of the conchiferan organization from an archetype similar to Textfigure 17 h via g to b, not the other way round. Thus they are decisive (Cf. p. 69) regarding a basic problem of molluscan morphology and shed light also on the preliminary stages leading to the phylum Mollusca—something I had foreseen since 1911, but for which I can only now provide the solution.

It is likely that the arms of cephalopods, much like similar appendages in other conchifers, are differentiations of an originally simple lateral edge of the foot, which were first formed in great number, with a very simple structure.

This view is the result of a reinvestigation of the entire development of cephalopods and general molluscan morphology; thus the presentation of my objects and the norms (Text figs. 8-17) deduced from methodical comparisons of observed facts should be taken as unbiased. As late as 1924 I was not able to make the decision

presented here, because I thought I was lacking certain arguments. Today I would not hesitate to begin with the diagram of Textfigure 10 e as an introduction to the presentation of molluscs in general, then showing its relation to Textfigure 6 i—so the presentation would gain in clearness.

A medial sagittal section may summarise the situation: Textfigure 42 shows the relationship between the embryonic body and the yolk sac; the latter contains only part of the yolk organ (the relative importance of that part being variable between species), the rest being enclosed in the embryo proper. During the constriction of the yolk by the arm crown, the distance separating the anus from the yolk sac has become very considerable (a highly significant, secondary condition). The separation of the cephalopodium from the visceral sac begins to become distinct; it can be visualized by a line drawn between the numbers 10 and 22 in the figure. The visceral sac shows total



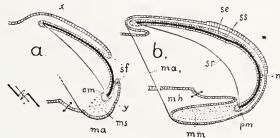
Textfigure 42. — Embryo of *Loligo vulgaris* (stage XI-XII). Diagrammatic medial section. 36× natural size. Morphological orientation.

1, 2: yolk; 3: yolk epithelium; 4: mesoderm; 5: ectoderm; 6: mouth; 7: rudiment of the poison [salivary] gland; 8: rudiment of the radula pouch; 10: dorsal part of mantle cavity; 11: mantle rim; 12: shell sac; 13: dorsal part of midgut rudiment; 14: position of shell sac closure; 15: posterior end of Hoyle's organ; 16: midgut cavity; (stomach) 17: muscular mantle; 18: ventral part of mantle cavity; 19: mantle rim; 20: position of prospective anal opening; 21: hindgut; 22: Vena cava; 23: ink gland; 24: funnel gland; 25: funnel tube; 26: prospective funnel tube opening, still closed by a thin membrane.

closure of the shell sac, and a moderately deep mantle cavity. Thus the anus is not yet covered by the muscular mantle, which extends from the edge of the shell sac, and anteriorly (at 10) the depth is even less. The gut anlage surrounds the inner yolk like a belt; it is drawn out into a peaked cap, which represents the hindgut, with an appendix (23), the ink gland rudiment. There is no direct connection with the stomodaeum. The posterior end of the latter is not in contact with the anterior parts of the midgut rudiment which join closely the yolk organ. A line drawn from 11 to 20 marks the longitudinal axis of the endodermal gut, which is now lying much higher than the mouth (Cf. Textfig. 17 h, g, b).

The funnel is newly closed to form a short tube (25); the outer yolk is completely enclosed in the yolk envelope. The latter is composed of an ectodermal epithelium (a modified epidermis) and a thin mesenchymal layer containing sinus-like spaces through which the yolk-resorbing bloodstream circulates. The resorption itself is carried out by the yolk epithelium.

The morphology of the newly-closed shell sac (Cf. Textfigs. 36-37) is of particular interest. Its correct comprehension is difficult since the shell epithelium becomes active long after the closure is achieved. In phylogenetic terms this represents a strong



Textfigure 43. — The development of the shell, the shell fold, the shell sac, the mantle cavity and the muscular mantle in their natural correlation, illustrated by diagrammatic medial sections of embryos of an archetypal (ideal) belemnoid form of cephalopod (cf. Textfigs. 42, 36 and 13).

a) x: growing anterior edge of the ostracum; y: growing posterior edge of the ostracum. The primary shell epithelium lying between these edges enforces the ostracum by the addition of thin layers (hyostracum). sf: shell fold, with a secondary shell epithelium producing enforcing layers (periostracum) added from outside. In the posterior part of the matrix producing the ostracum (om), the cell material for the formation of the muscular mantle (ms) is concentrated; in its present, modest mass it still is reminiscent of a normal, soft mantle rim of gastropods (Textfigs. 13 and 16). In the latter, muscular differentiations as well as skin extensions can be formed by the soft mantle rim, since the shell edge is often situated in a sharply demarcated gutter, the "shell groove".

b) The mantle cavity (mh) has been formed by a combination of invagination and growth of the mantle; the position of the anus (arrow) thus comes to lie inside the cavity. Shell growth was lower on the ventral side, however, whereas the soft mantle rim has been accelerated in the form of a really muscular mantle (mm). The primary mantle, which lies on the inner surface of the shell, is formed in certain parts only, namely dorsally, i.e. in the nuchal area, and laterally; ventrally a minor rudiment (pm) is inferred that corresponds to the large terminal cone (phragmocone) of fossil cephalopods (cf. Textfigs. 22 and 30). This rudiment is lacking in the extant types.

heterochrony. The shell is a formation that already characterizes three preliminary grades (Mollusca, Conchifera, Cephalopoda) leading to the dibranchiates, whereas the well-established muscular mantle is a particular feature of the dibranchiates. One gets the impression that the shell fold covers an imaginary shell by closing over the shell epithelium that will later form the shell. The phylogenetic process, i.e. the series of sequentially achieved stages in the respective ancestral forms, must of course have been different, and even in the ancestor of modern cephalopods the formation of the shell fold probably has been based ontogenetically on the existence of a normally formed primordial shell, which must have been differentiated according to the typical conchiferan mode (Textfig. 13). (Unfortunately we do not know the embryonic development in *Spirula*, which might show archaic features). The processes likely to have occurred in primitive dibranchiates, from which the ontogeneses of modern forms can be derived, are illustrated in Textfigure 43.

CHAPTER 4

The Typical Course of Later Embryonic Development in Dibranchiates

Contents: 6th period: a. secondary shifts in the head complex, b. further shaping of the embryo (p. 129). 7th period: The final growth of the embryo and its behaviour inside the egg envelopes (p. 140).

In the preceding chapter a number of very interesting and important reminiscences of cephalopod phylogeny have been presented, some of which point at much older processes of precoelomatic stages (theory of mouth and anus formation), or which have at least to do with the grades leading to molluscs (primary foot) or to the conchifers. In addition to those reminiscences we have seen, from early stages onward, special cephalopod features, and further dibranchiate characters which were not at all correlated to stage. The following sections deal exclusively with such special features, following the description of development that leads to the cephalopod, and often to the dibranchiate condition.

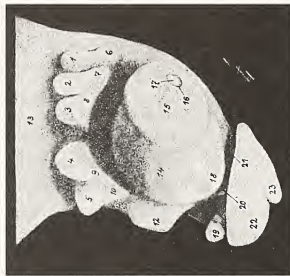
6th Period: a. Secondary Shifts in the Head Complex

At the stage shown in Figure 12 of Plate 2, we can already distinguish two components in the arm rudiment, a basal one and a distal one. The distal section is directed forwards and outwards and represents the arm proper, which will be formed by

growth in length. The proximal section is a sort of pedestal attached to the head, to which otherwise it shows no closer relationship.

We remember that in *Nautilus* (Textfigs. 26 and 27 a) a similar distinction was made in each arm: The basal part forms the sheath, the distal section being the cirrus (Vol. 1, p. 61). In *Nautilus* already the sheaths reach far back on the head, enclosing it completely in their muscular mass; the hood belongs to that as well. Their projecting edges surround the eye ball, which is thus sitting in a depression, a sort of primitive orbital cavity, in which the eye with its stalk has a certain mobility. The surrounding arm parts represent a protecting wall for the eye; it is thus sheltered from external harm despite its prominent insertion, since the outer surface of the eye chamber lies at the same level as these arm parts. This has to be remembered when the following morphological facts are discussed:

120 In the dibranchiates also the basal parts of the arms, which will be termed "arm pillars", reach backwards on the head to which they become fused on the dorsal surface and on the ventral surface. On the latter, one thus always finds the arm pillars of the 2 ventral arm pairs; on the dorsal side the remaining ones are situated, i.e. 2 pairs in octopods, 3 pairs in decapods. This fact (compare Pl. 4, Fig. 7 with Pl. 28, Fig. 1)

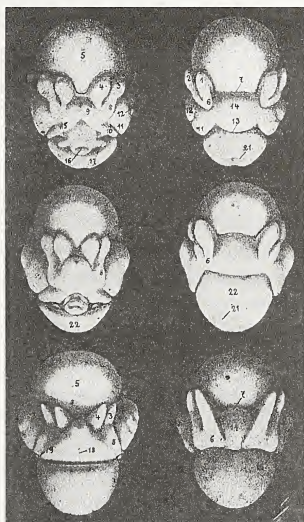


Textfigure 44. — Embryo of *Loligo vulgaris*, in lateral view, 56× natural size. — The stage (XI) corresponds to the one shown in Textfigure 40, and is close to that of Textfigure 42 (See also Pl. 4).

1-5: arm rudiments; 6-10: rudiments of arm pillars; 11: gap between the 3 dorsal and the 2 ventral arm rudiments; 12: funnel tube, not yet complete; 13: yolk sac; 14: mass of ocular stalk, very swollen due to the rudiments of the white body optic ganglia contained inside; 15: eye ball; 16: iris fold; 17: primary cornea with the eye lens projecting inside (Textfig. 39, d: 1); 18: cheek hump; 19: gill; 20: funnel retractor; 21: funnel pouch; 22: mantle sac, still rather flat, bowl-shaped; 23: fin.

The embryo is orientated according to the adult swimming position: mantle posteriorly, arms anteriorly directed. Note the arm crown embracing the eye from the anterior side, extending backwards around the eye above and below.

allows one to recognize homologies between the arms of decapods and octopods: The two ventral pairs correspond perfectly in their respective positions; in octopods apparently one of the dorsal pairs seen in decapods is missing, probably the first one. In any case the ventrolateral arm which forms the tentacles in decapods (Pl. 17) is present in the octopods (Pls. 28, 29); thus one cannot consider the octopods as decapods devoid of tentacles (Cf. Vol. 1, p. 660). The eye is inserted between the dorsal and the ventral arm pillars, and the positional relationship of the pillars to the eyes will soon be very similar to the relation between arm sheaths and eyes in *Nautilus* (Text figs. 44, 48).



Textfigure 45. — 3 embryos of *Argonauta argo* (stages XII, XIII, XVI) in dorsal and ventral view. 40× natural size. Note especially the secondary covering of the head by the arm pillars growing posteriorly (6 and 8).

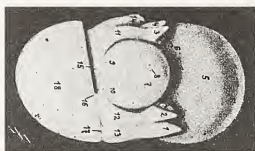
1-4: arm rudiments; 5: yolk sac; 7: position of the (entirely closed) mouth; 9: funnel tube, just formed; 10: funnel pouch; 11: cheek hump; 12: eye; 13: dorsal mantle cavity, a furrow-like rudiment (here not progressing in depth); 14: position of cerebral commissure; 15: funnel retractor; 16: anus, not yet open; 17: gill; 18: funnel tube seam; 19: olfactory tubercle; 20: connection between the head covers (6: i.e. the broadening arm pillars) and the muscular mantle; 21: fin rudiment (cf. Pl. 27, Fig. 9); 22: mantle sac in the area of the subsequently penetrating (from the two sides) dorsal mantle cavity.

The individual arm pillars can be very distinct from one another and from the head anlage; but in many instances the limits are less well defined, so that the following observations are not always possible with equal clearness. Textfigure 45 provides a rather clear impression of their further development, especially on the dorsal head surface. One can see how the partly fused arm pillars move backwards on the head, becoming broader during this process, so that a large part of the top becomes covered with a thick cushion that replaces the primary head cover. Finally (Pl. 35) they unite dorsally, reach to the mantle rim and cover the entire dorsal head surface except the bulging eyes. Similar processes take place on the ventral side, except the large funnel and the two areas (in more posterior position in octopods) where the olfactory organs will be formed. (For the decapod conditions see Pls. 17 and 18.)

At subsequent stages the term arm pillar becomes inappropriate (since a distinction of the different arm-related parts of the secondary cover is no longer possible), and the term "head covers" will therefore be used. In the literature one finds statements suggesting that the arms form a circumvallation of the head, something that may generate rather vague ideas. The situation described above was hitherto unknown; it was indeed not easy to demonstrate. (Cf. Lang, *Mollusca*, p. 447, where earlier, incomplete, morphologically insufficient descriptions of these processes are cited; and above p. 114.)

The secondary head covers leave open three important sections of the primary head anlage: 1) the mouth, 2) the eyes, 3) the olfactory tubercles.

As for the mouth we have seen (Textfigs. 25, 34, p. 80, 105) that its primary position is between the dorsal arm rudiments, and that this position is conserved when the



Textfigure 46. — Advanced embryonic stage of *Argonauta argo* (stage XVI). 50× natural size. Note the nearly complete covers of the head (11, 12, 13), which lies now very close to the eye, facing it with their lateral edges from which the primary lid will be formed.

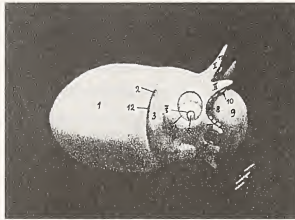
1-4: arms; 5: yolk sac; 6: papillar sucker rudiment; 7: eye ball; 8: iris fold; 9: posterior end of the ventrolateral edge of the head cover; 10: posterior end of the dorsolateral edge of the head cover (subsequently connected with the former, via an intermediary fold, to form the prospective primary lid); 11: arm pillar of third arm; 12: arm pillar of second arm; 13: arm pillar of first arm; 14: funnel tube; 15: olfactory tubercle; 16: end of mantle aperture, which is fused in its dorsal part (17); 18: mantle sac.

dorsal arms move closer towards each other (Textfig. 40). This situation is typically maintained during the formation of the arm pillars, although the space left for the mouth becomes increasingly narrow (Pl. 4, Figs. 3, 9; Pl. 16). But finally the two dorsal arms with their pillars become fused to each other above the buccal opening, thus replacing the small medial strip of primary head cover that had persisted so far. This is not a continuation of the shifting (p. 104) undergone by the whole arm crown (which has already come to an end); it is a special process finishing the secondary head covering. It places the mouth in a position that is typical for cephalopods only, i.e. in the center of the arm crown which can be viewed as the homolog of the gastropodan foot. At early stages (Textfig. 40, Pl. 26) the mouth has the normal position, and the surrounding part can be viewed as the preliminary stage of a typical molluscan snout (Cf. Pl. 28).

If this process were to be summarised by the statement "the foot grows around the head", it would have to be rejected. For here the dorsal arms grow only around the mouth, or perhaps the anlage of the snout, not the head as a whole. Unfortunately the confusion between head and snout is current in molluscan literature!

The relation of the lengthening arm bases, the arm pillars and the resulting head covers to the eyes are of special interest, and here again a generally accepted, erroneous representation has to be rejected (Cf. Lang, 1900, Mollusca, p. 266, Fig. 251): According to this representation the eye and its accessory parts are formed by three or four successive circular folds that are arranged concentrically. In fact the eye proper is constituted by the process illustrated in Textfigure 39, and the primary and secondary lid folds are quite heterogeneous, much younger components of the optic organ of dibranchiates, which are essentially derived from the arm complex in a rather complex way; they are not formed by simple circular folds surrounding the periphery of the eye. It is true that at later stages (Textfig. 47) all dibranchiate embryos (Pls. 6, 11, 19, 30, 36) show a ring-shaped fold surrounding the eye proper; I call it the "primary lid"; but this formation has a very peculiar origin:

It has already been emphasized (p. 122) that in *Nautilus* the arm bases form a protecting wall around the eye ball and thus form a primitive orbital cavity, in which the eye can move rather freely. Furthermore, we have seen that the arm rudiments of dibranchiates surround the eye mass in quite analogous fashion, orientating certain parts to each eye (Textfig. 44): These are: 1) the outer edge of the dorsolateral arm pillar (here I consider the arm pillars in correspondence with the octopod arms), 2) a generally rather indistinct connecting piece between the dorsolateral and the ventrolateral arm (Pl. 23,



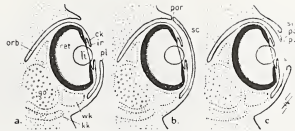
Textfigure 47. — Far advanced stage of *Argonauta argo* (stage XVIII-XIX); this animal hatched prematurely after stimulation (shaking) but was perfectly viable (cf. Pl. 36). 40× natural size.

1: mantle sac; 2: olfactory tubercle; 3: funnel pouch; 4: funnel tube; 5: primary lid; 6: lens; 7: iris fold; 8: arm web between arms II and III; 9: yolk sac; 10: sucker; flagellar tip of first arm.

This figure shows the typical primary lid rudiment of dibranchiates, and the (juvenile) octopodan correlation of the mantle slit, nuchal fusion, olfactory organ, funnel pouch, funnel tube, eyes and arms with suckers. The oval body outline is characteristic for the argonautids, the special predominance of the dorsal arms is typical for *Argonauta*.

Fig. 2, 3) the outer edge of the ventrolateral arm pillar. These structures first surround the eye only from the anterior side, reaching only a short distance dorsally and ventrally. But with the progressive enlargement of the pillars they reach ever farther around the eye and finally (except in sepioids) nearly meet behind the eye; but they never meet entirely. They stop short of that potential meeting point (Pl. 6, Fig. 7 v-d; Pl. 34, Fig. 7). On the separating piece that represents part of the primary head cover, a very delicate fold rises and unites the two pillars, thus completing the ring. In the sepioids (see there) this connecting fold is quite sizable, in contrast to the normal condition of teuthoids and octopods. I call it the "posterior connecting piece" of the lid fold (the anterior connecting piece being the modest elevation of the arm crown
125 between the dorsolateral and ventrolateral arms). Thus 4 components can be identified in the circular fold that forms the lid and corneal complex in dibranchiates: 1) the posterior connecting piece which belongs to the primary integument of the head, 2) the anterior connecting piece which belongs to the arm complex, 3) the outer edges of two arm pillars. It should be recalled that the fourth arm of decapod embryos forms the tentacle, which thus takes a special part in the formation of the primary lid and the cornea.

The 4 components combine in a secondary unit (Textfig. 47), which no longer indicates its heterogeneous origin, and which is capable of further quite diverse differentiations.



Textfigure 48. — Diagrammatic frontal sections through the right eye. a) General juvenile state (persisting in the oegopsids). b) Loliginid condition. c) Octopodan condition. See also Volume 1, page 96. — orb: orbital cavity; go: ocular ganglion; ret: retina; li: lens; ir: iris; ck: ciliary body; pl: primary lid; por: orbital pore; sc: (secondary) cornea; sl: secondary lid; po: primary upper lid; pu: primary lower lid.

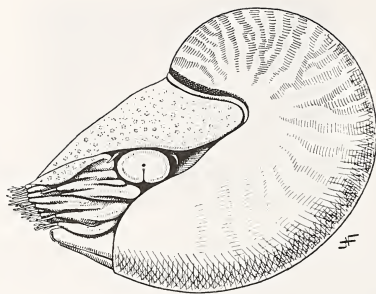
Diagram shows the archetypal form of the primary lid as generalized in juveniles; as far as is known it persists only in oegopsid squids and in *Spirula* (the only pelagic-nektonic sepioid). It is remarkable that a similar condition can be produced artificially (via a process of partial growth inhibition) even in *Sepia* (See concluding chapter).

The posterior connecting piece of the lid (Textfig. 46) shows a remarkable positional relationship with the olfactory tubercle: The latter lies in very close vicinity of the eye, much like its homolog in *Nautilus*; it is positioned behind the eye (shifted slightly ventrally in decapods) and is a derivative of the primary integument of the head. The posterior ends of the pillar edges finally position themselves in such a way that the connecting fold separates the developing tubercle from the eye: It thus comes to lie outside the eye complex, on the open surface of the head. In *Nautilus* the orbital pit remains totally open posteriorly, and there is no hint of such a separation.

This separation thus appears to be a secondary feature of the dibranchiates, which are characterized by the completion of the orbital pit and its limitation by the 126 posterior connecting piece of the lid. The other parts of the eye lid can be considered equivalent to the parts present in *Nautilus*, so the development of the lid can be viewed as an elaboration of the more primitive eye protection provided by prominent arm bases.

The arms involved cannot be individually homologous; the numbers make this impossible. Similarly, the conditions just described for the dibranchiates cannot be derived directly from *Nautilus*; instead a less specialized cephalopodan prototype must be considered (Textfigs. 21 and 28) as the common morphological basis.—But we note already the interesting case of a correspondence of primary ontogenetical conditions with the supposed homologous conditions of a very ancient form.

Of course the phylogenetic interpretation of these processes can be pushed much farther. Following the considerations presented on page 42 we can consider a com-



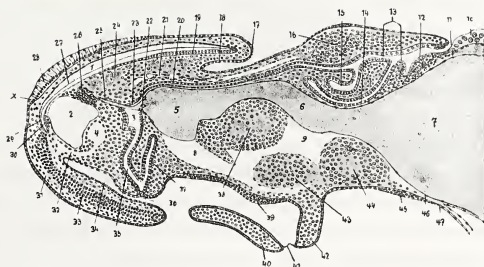
Textfigure 49. — Lateral view of *Nautilus pompilius* in swimming position. Drawn after a preserved specimen, one half natural size (from Vol. 1, p. 55). Note the elbow-shaped arm bases flanking the eye, thus contributing (together with the mantle and shell rim, and with the funnel pouch) to the formation of a primitive orbital pit.

plete series of transitional forms which first prepared ground for the typical conditions of cephalopods to be realized and subsequently elaborated in those of the dibranchiates. A comparison of Plates 33 to 36, especially the lateral views, will provide an illustration.

We conclude this section in giving again a midsagittal section to summarize the
 127 embryonic organization (Textfig. 50). This section represents a stage (XIII) at which the processes described are still far from being completed (Cf. Pl. 6, Fig. 4), but it is particularly useful to illustrate the bauplan of an essentially complete cephalopod.

The visceral sac is markedly stretched compared to the stage shown in Textfigure 42, and its separation (by constriction) from the cephalopodium is very distinct. (To localize the separation draw a line from 18 through 8 to 37). The primary longitudinal axis is still clearly marked by the endodermal gut (23-3-35). The latter is now (at point 22) in open connection with the stomodaeum (oesophagus, 20), at a point considered homologous to an anterior remainder of the blastoporus as in other molluscs and coelomates, which could thus be called a pharyngeal orifice (Textfigs. 9, 14).

The plug of the inner yolk (5) is strongly constricted and is connected to the outer sac only by a thin strand (6) which passes through the pharyngeal ring (16, 44). The mouth (11) lies closely above it; it is still open to the outside but will be closed soon by the bases of the dorsal arms (Pls. 5, Fig. 2 and 6).



Textfigure 50. — Medial section through an embryo of *Loligo vulgaris* at stage XIII (Pl. 6, Fig. 4), slightly schematic. — 90× natural size.

1: shell sac; 2: coelom; 3: stomach; 4: heart; 5: inner yolk sac; 6: connection with outer yolk sac (7); 8: vena cava; 9: sinus cephalicus; 10: cells of the yolk sac ectoderm; 11: mouth; 12: position of the beak and inner lip rudiments (cf. Textfigs. 42 and 63); 13: subradular organ with the outlet of the poison gland (14); 15: radula pouch; 16: cerebral ganglion (commissure); 17: dorsal mantle rim; 18: position of prospective nuchal attachment; 19: matrix of the proostracum or free rachis of the gladius; 20: foregut; 21: Aorta anterior; 22: terminal part of the inner yolk sac; 23: dorsal part of the stomach epithelium (endoderm); 24: sinus posterior; 25: genital strand; 26: gonad; 27: shell membrane; 28: Hoyle's organ; x: position of shell sac closure; 29: cone matrix; 30: siphuncular rudiment; 31: mesenchyme of subcutis; 32: Aorta posterior; 33: muscular mantle; 34: ventral mantle cavity; 35: hindgut; 36: anus; 37: ink sac; 38: pleurovisceral ganglion; 39: funnel gland; 40: funnel tube (level of fusion); 41: hymen of funnel tube orifice; 42: dorsal part of funnel; 43: statocysts (separating wall); 44: pedal ganglion; 45: ectoderm of head; yolk epithelium; 47: ectoderm of yolk sac.

6th Period: b. Further Shaping of the Embryo

The developed primary lid contracts over the eye, more or less rapidly, but in such a way that it remains open for a long time, the width of the opening being controlled by its marginal musculature. The further differentiation differs markedly between groups and will not be followed any further here (Pls. 19, 30, 36).

The olfactory tubercle shows different elaboration in octopods and decapods. While in octopods it always occupies a modest part of the primary head cover (Textfigs. 45, 46), the opposite occurs in decapods, where the anlage is an ill-defined epithelial thickening situated on the ventrolateroposterior surface of the head, contracting slowly (Pls. 5, 17, 18) to form a small, oval cushion similar to that existing in the octopods; it then lies ventrally behind the eye, on a bulging part of the head which

we call the cheek hump. The anlage appears in this form in all the juvenile types of decapods, no matter what its definitive shape, and we therefore suppose this to be the primitive form of the organ according to the considerations given on page 40. It represents a differentiation of the primary, sensory epithelium of the head, with a specialization of the sensory function.

From their papilla-like anlagen, the arms grow out in length, the tapering tip forming a vegetational point, from which continuously new material is added to the anlage, while the proximal parts undergo histological differentiation. The first steps of sucker development and rearrangement can now be observed (Pl. 21). In adult cephalopods
128 suckers indeed show very diverse forms and arrangements (vol. 1), but they always develop in a way that indicates a fundamental congruence in the main features.

Sucker rudiments first appear as solid papillae, without any indication of a sucking chamber, in contrast to what could be expected given the importance of this component. They are always formed in single file, even in forms where later they will be arranged in 2, 4, 8 or more rows. This observation leads to considerations about the genetic-morphological factors allowing one to "derive" the complicated arrangements from the single file condition: Each sucker had a well-defined position in the single file, and its identification is of great importance in a morphological analysis, e.g. of the tentacular club. A further peculiarity of the sucker anlagen is that instead of being round papillae as could be expected given their later form, they are transverse, ridge-



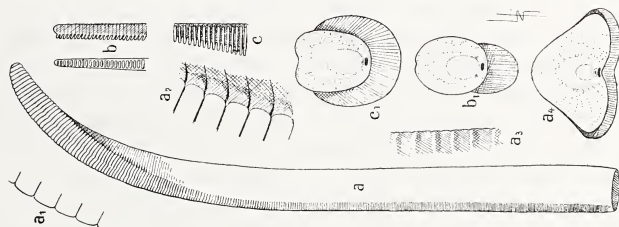
Textfigure 51. — Arm tip of a juvenile *Eledone*. 24× natural size. — Compare with Plate 21, Figure 4. — Note the arrangement of sucker rudiments proximally from the extremity that is devoid of growth cone. The bulges separated by transverse furrows become increasingly rounded papillae, in the center of which a small depression will subsequently appear as the rudiment of the suction chamber.

like papillae. This could be due partly to momentary space limitations; but one should not forget that this feature is strikingly similar to what we see in *Nautilus* (Textfig. 52), where the primitive adhesive organs are transverse ridges on the cirri; they are arranged in single file and are flattened against one another.

In some instances the number of sucker rudiments in single file (before rearrangement) is considerable; this occurs wherever a relatively large number of adhesive organs has to be formed rapidly (Pl. 16, Fig. 4; Pl. 21, Fig. 8); for example, on the tentacular arms of sepiids or on the hectocotyli of argonautids (Vol. 1, p. 746). More often, howev-

er, one finds a short, single row grading into early rearrangement towards the proximal end. The first step is generally a zigzag arrangement, so that alternating suckers lie in two parallel rows; the general impression is that this modification is caused mechanically by the growth of the anlagen, which no longer find sufficient space in a row.

Often the process described is repeated once or several times, the two rows of alternating suckers doing together what the single row did at the outset, resulting in arrangements with 4, 8, 16 or more rows (Pl. 21). Rarely does the rearrangement follow a different pattern: Thus *Heteroteuthis dispar* shows a sucker arrangement in 6 rows on the tips of the ventral arms, resulting from a 2-row arrangement through zigzag formation of groups of three suckers. In histioteuthids the tentacular manus has its suckers arranged in 7 rows, without any hint of a loss of suckers after a conceivable 8-row arrangement. All other arrangements are derived from sucker patterns with 2 to 32 rows, secondary modifications always being possible. The tentacular clubs of sepiolids and other decapods often show conditions that are difficult to analyze.



Textfigure 52. — (From Vol. 1, p. 63). — Brachial cirri of *Nautilus pompilius*. a) Cirrus from the outer arm crown (prehensile arm); $8/3\times$ natural size. a₁) Detail of former in profile, at higher magnification. a₂) Transition between inner and outer surface, at same magnification as a₁. a₃) Detail of proximal part in profile, same magnification. a₄) Cross section of distal part, same magnification. b) Cirrus of palp, comb-like; inner and lateral aspect, $8/3\times$ natural size; b₁) Cross section. c) Cirrus of arm (tip); $8/3\times$ natural size. c₁) Cross section. — In the cross sections, one can distinguish the arm and the adhesive pad, in the former one sees the nerve with its oval outline in cross section, below it lies an artery, below the latter a vein (black). Note the different shapes of the adhesive pads.

Quite often the suckers are arranged in zigzag immediately after their formation, so that single file development continues but is barely recognizable in the result, or only towards the end of development. The arm tip continues to grow for a long time and forms new sucker rudiments continuously, so that the number of suckers increas-

es with the age of the individual. In large individuals of *Octopus macropus* one finds up to 300 suckers on each arm; in half-grown individuals there are just about half as many (Cf. vol. 1, p. 703). Often it is difficult to determine whether the variants with more or less suckers are typical, especially since damaged arms and regenerates are encountered frequently. In decapods the situation is similar; but in general the number of suckers seems to be more typically limited.

Evidently all these secondary modifications of arms and suckers can be interpreted phylogenetically, and we leave it to the reader to consider such interpretations. One opinion has to be avoided in such attempts, however, namely that here development in
130 general has been synthetic:

It is easy to show that in certain groups a more complicated sucker arrangement than the one now observed was archetypal (more on that later on).

The anlagen of the buccal arms or buccal funnel (which represents a rudimentary arm crown; cf. Vol. 1, pp. 99, 179) often appear very late in development, and rather indistinct; in the octopods they are no longer formed.

These buccal arm rudiments are low, papillar elevations of the skin (similar to the early arm rudiments) inserted between the yolk sac and the surrounding arm rudiments (Pl. 21). In the decapods they are associated with the bases of the sessile arms, the dorsal 4 shifted slightly upwards, the ventral 4 shifted slightly downwards and medially. No such rudiment is (any longer) associated with the tentacle. The 8 papillae represent the anlagen of the buccal lappets and are connected with one another by low ridges, which will become umbrella-like membranes in the course of buccal arm growth. The two mediodorsal rudiments are separate in the beginning, and one has to recall that the mouth has been shifted between them, so that a primary unpaired anlage is highly unlikely. But when they become distinct they are already situated above the mouth and soon become more closely connected with each other than any of the other 6 rudiments. In most cases they become fused, forming a single, unpaired mediodorsal lappet. This does not happen in the family Enoploteuthidae, and I have found instances of inhibition, with two distinct lappets, in other forms as well (Pl. 21, Fig. 3).

The dorsal buccal lappets are an interesting example for the capacity of organic formations not only to divide, but also to fuse, and for the possibility that such a process, occurring as an exceptional process, can become a new (derived) norm.

We have seen that the mouth opening has moved downwards, passing between the dorsal arms and buccal lappets (Pl. 21, Fig. 1). It thus lies inside the arm crown and buccal funnel, closely applied to the yolk neck (Textfig. 50). This becomes particularly

clear when the latter becomes constricted somewhat more distally (Pl. 21, Fig. 3), an early process that can finally lead to yolk sac autotomy (*Sepia* and others). The buccal orifice is now strikingly small, since its edge is strongly contracted; it will soon be covered completely by the buccal funnel and thus becomes invisible to the observer, even if the buccal field is artificially opened up by removal of the yolk sac (Pl. 22).

- 131 When the buccal funnel is cut open (Pl. 11, Fig. 4), the mouth opening becomes again visible, and one can then see that reduction of the yolk mass allows it to grow in size until it fills the circle of the buccal funnel entirely, once the yolk sac has disappeared (Pl. 22, Figs. 3-7).

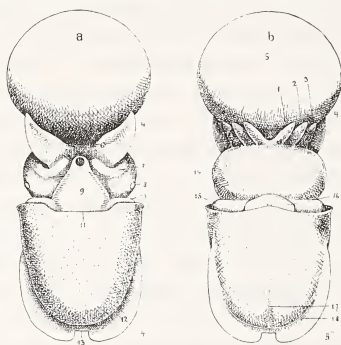
During this process the primary edge of the mouth opening grows wider and forms what we call the outer lip at the adult stage. It is a rather simple, smooth-rimmed circular fold, which tends to be overlooked despite its original importance. In fact, a secondary circular fold that rises from the inner wall of the buccal cavity (or stomodaeum), thus lies inside the above-mentioned outer lip, has become more voluminous (Textfig. 50) and has grown beyond the edge of the former; this "inner lip" now forms the actual rim of the mouth opening. It is much thicker and its edge is covered with several rows of small knobs. Inside this lip the beaks often can be seen, especially the lower beak, and when the beaks are gaping, one can look into the buccal cavity, from which the subradular organ and the radula project (Textfig. 84).

The funnel complex was already laid out at stage X. (Cf. Pl. 17, Fig. 2 and Textfig. 38). We left (p. 112) the anlage when it began to insert itself into the mantle opening. The seam uniting the funnel tube lobes (Pl. 17, Fig. 8) forms rapidly from the anterior tube end in a posterior direction and finally disappears from the surface aspect (Pls. 4 and 5). Laterally the tube is united with the funnel pouches; their separating wall, the funnel septum, extends as a ridge towards the deeper part of the mantle cavity and attaches dorsal to the base of the gill (Pl. 17, Fig. 5). This extension is the anlage of the funnel retractors and indicates, up to the adult stage, the composition of the respiratory and swimming apparatus from heterogeneous elements. The archetypal insertion (in cephalopods) of these muscles is on the shell margin, at the transition between the conotheca and the proostracum; wherever the shell becomes rudimentary, corresponding parts of the muscle mantle provide the necessary support.

The funnel pouches do not require any special differentiation other than their concave structure allowing them to form pouch-like valves. Inside the funnel tube, however, accessory structures are formed later on, namely the funnel valve and the funnel gland. The funnel valve (Pl. 18, Fig. 3) forms a roundish lappet projecting from the

muscular background, close to the funnel opening; later it will prevent influx of water through this opening (Textfig. 84). Its formation is suppressed in the octopods; it is present in *Nautilus*.

The funnel gland is a mucous gland, probably serving in the management of the funnel opening (protection against abrasion); it is typically composed of 3 parts, all of which appear as glandular, gill-like thickenings of the epithelium (Textfig. 50). The middle part (Pl. 18, Fig. 3) lies on the dorsal wall of the funnel, behind the funnel valve, and tapers into two diverging posterior branches. The two lateral parts (Textfig. 68) are oval and lie on the ventral funnel wall, slanting posteriorly and inwards. Their posterior ends can be fused with the branches of the middle part, so when the funnel is cut open, a W-shaped pattern appears (Cf. Vol. 1, pp. 102, 181, 672).



Textfigure 53. — Advanced embryonic stage of *Sepia officinalis*; 8× natural size. — See Plate 18.

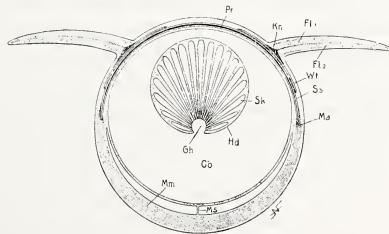
1-4: arm rudiments; 5: yolk sac; 6: buccal funnel from which the yolk stalk emerges; 7: tentacular stalk in its (progressively differentiating) pouch, visible through the integument; 8: olfactory tubercle; 9: funnel tube; 10: funnel pouch; 11: funnel depression of the mantle rim; 12: fin; 13: connecting edge of the fins, occupying the position of the (lacking) body tip; 14: pupil (visible through the cornea); 15: funnel pouch; 16: nuchal attachment; 17: Hoyle's organ, medial branch; 18: lateral branch.

The nuchal attachment (16) is exposed after separation from its counterpart (due to the formation of gas in the shell sac, generated by an acid fixative).

A differentiation that again has been lost in octopods is the nuchal attachment. It is part of the funnel apparatus, in which it is integrated not only due to its original topographical relationship (Textfig. 38) but also for its functional cooperation. It forms from a finely rimmed elevation of the epithelium lying dorsally between the

funnel pouches; it can be variously complicated in structure at later stages, forming the adhesive and gliding surface that is the counterpart of the opposing inner part of the dorsal mantle rim. The latter is typically supported by the proostracum, hence part of the true primary mantle, which is replaced partly by the secondary or muscular
 133 mantle (p. 119) only later, in a clearly atypical fashion. The special part facing the nuchal attachment is the functional antagonist of the latter and can be termed the "col-
 lar attachment" (Cf. Vol. 1, pp. 100, 123).

In the representation of the mantle sac, two components must be distinguished even though they may not appear distinct from the outside: The shell fold with the developing shell lying underneath, and the muscular mantle.—The embryos of oegop-
 sids (Pl. 8) show this distinction in a particularly clear and typical form, in that the shell is spoon-shaped, embracing the posterior part of the body; the anterior end of the shell is drawn out into a still-short proostracum, whereas the muscular mantle is inserted on the shell or shell sac all around its periphery, thus forming an almost tube-
 like, gutter-shaped plate.—In all the other dibranchiates studied the muscular mantle appears very enlarged at the expense of the shell sac even at early stages, pushing its inserting margins more or less drastically over the outside of the shell sac, so that the shell (appearing dark in the pictures) no longer, if at all, appears in its entirety; (Cf. Pl. 5, Fig. 9; Pl. 8, Fig. 8).



Textfigure 54. — Diagram illustrating the connection of the shell (Pr), the fins and the muscular mantle in dibranchiates (from Vol. 1, p. 114). Imagine a cross section made in the area of the living chamber of a belemnoid form (Textfig. 28), cutting ventrally through the muscular mantle anchored on the shell rim, and dorsally through the shell wall (Pr) at the transition to the proostracum. Starting from this level, the fins reach more caudally and thus lie mostly on the outside of the phragmocone (cf. Textfigs. 53, 60).

Kn: fin cartilage with gliding surface; Fl₁, Fl₂: antagonistic layers of the fin; wt: articular pouch of the fin base, derived from the shell sac (Ss) by evagination; Ma: insertion of the muscular mantle on the shell rim; Sk: sperm canals; Hd: testicle; Gh: testicular cavity; Co: coelom; Mm: muscular mantle; Ms: mantle septum.

The fins, which are formed on the outside of the shell sac (p. 109), conserve their original position at least in their posterior part, which generally tends to degenerate slightly. The anterior, progressive part will grow over the outer surface of the muscular mantle, to which the articular connection with the shell sac will then be transferred. The lateral branches of Hoyle's organ reach partly over the fins, always closer to their 134 posterior edge (Pl. 7, Fig. 3; Pl. 8, Fig. 8; Textfig. 53). The further modifications of this organ (Cf. p. 110) are of interest only in a very special context.

The body surface remains generally smooth. (Concerning skin spikes in octopods and integumental warts in sepiids, see the respective section). Certain integumental differentiations, which I call glandular lines, are generalized features (Pl. 18, Figs. 1; Pl. 23, Fig. 6, 8; Pl. 30, Fig. 3). These are delicate longitudinal ridges that appear rather early on the outside of the arm rudiments, roughly where the fine groove appeared at much earlier stages. These ridges move onto the head surface with the arm pillars (head cover), reaching backwards nearly as far as the latter. They are particularly distinct on the three dorsal arm pairs of decapods and later represent a voucher for the covering of the primary head anlage by the epithelium of the arm bases. Possibly they are the forerunners of the later swimming membranes, which would then have a more general significance than supposed earlier (Textfig. 28), in that they were common to all arms in decapods as well as in octopods. (Cf. vol. I, Fig. p. 110). Clearly, the swimming membranes, wherever they occur, are formed in the same orientation as the glandular lines.

The chromatophores will be considered in detail in the context of an embryological and anatomical description of the skin. Here their role in the external aspect of the animal is of interest. They appear rather early as colored patches. Especially in some oegopsids they are visible, as shown by Grenacher (1877) even before the outer architecture of the embryo (as in Pl. 8, Fig. 1) becomes distinct. In the sepioids, octopods and loliginids which I have been able to observe, these outer structures appear much earlier than the chromatophores. From their beginning, two categories of color patches are distinguishable, light ones and dark ones. The former are light yellow to orange yellow, the latter orange red, yellow brown, red brown to sepia brown.

The structure of the mantle cavity itself can be followed in Plates 17 and 18. One can see stepwise how the gill anlagen move inside along with the anal papilla that lies between them (Cf. Pls. 4 and 5). While the depth of the mantle cavity increases, a narrow connecting membrane persists between the body and the mantle, so that the deepest

part is bipartite; this membrane is the "mantle septum".—The funnel retractors lie above the base of the gills, tapering out first on the middle piece (body trunk), later becoming inserted on the shell and mantle (see above). Further dorsally, but still close to the base of the gills, large oval thickenings formed from the epithelium of the muscle mantle can be seen already at early stages (Pl. 17). These are the rudiments of the stellar ganglia (Pl. 17, Fig. 5). Further dorsally the mantle cavity turns very shallow so that between the neck and the muscular mantle remains a simple slit, which later will be largely occupied by the nuchal attachment.

Thus the general topography of the mantle cavity is outlined, and we can now turn to the details of its further development: by growing increasingly deeper in relation to the longitudinal growth of the mantle, the mantle cavity and its components undergo various modifications, and new anlagen become visible:

The gills first appear as simple papillae that are slightly drawn out laterally and flattened dorsoventrally (Pl. 17). The round end then grows out slowly, resulting in a finger-like, slightly compressed structure. In either side a rounded ridge contains the developing gill vessels, the afferent in the outer edge, the efferent in the inner edge.

The plate lying between these edges slowly takes a pointed triangular shape (Pl. 17); it is a thick integumental fold lying between the boundaries of the vascular edges that already shows some complex structures: in fact this fold is larger than the boundaries and fits in the latter only by pleating itself. Thus a number of small transverse folds are formed from the base to the distal end of the plate, appearing as ribs that alternate with grooves on both the dorsal and the ventral surface of the gill anlage, leaving only a smooth edge. The projecting parts represent the anlage of the gill lamellae, which are not projections rising from a solid base but pleats involving the entire respiratory surface. This process is not easily visible in the figures.

The embryonic gill thus formed (Pl. 17, Figs. 5 and 8) represents the basic form of a molluscan "ctenidium". The typical development of a ctenidium produces (at least as a transitory feature) a narrow base inserted close to the mantle furrow, but still on the body, i.e. on the shifted mantle cavity roof, without an attachment to the mantle; this can be considered a phylogenetically primary feature. But already at the stage shown in Figure 8 of Plate 17, a delicate skin fold runs from the gill to the mantle; it comes from the outer edge of the gill and tapers out slightly ventrally from, close to the stellate ganglion; this is the anlage of the gill attachment. At the outset it is situated at the gill base, similar to *Nautilus*, but even less developed; it is shifted forward

much later in development, often only at postembryonic stages; it finally attaches the large part of the gill longitudinally to the mantle (Pls. 17, 18, 19, 20). In the outer edge of the gill anlage, not only the afferent gill vessel is formed; more laterally (pushing the vessel more to the medial axis) a parenchymatic body, the branchial spleen is formed; it appears as the mechanical axis of the gill, also providing the base for the gill attachment (Pl. 20, Fig. 3). The proximal gill lamellae are characterized by an asymmetry in that they do not reach medially to the efferent vessel so that they can get
136 only an indirect connection with it.—Much like the arms, the gills continue to grow at the apex, forming new lamellae so their total number can become rather high.

Each gill lamella of the first order begins as a triangular fold similar to the early gill anlage as a whole, but less pointed than the latter; the outer edges contain the afferent and efferent vessels that correspondingly branch off the primary vessels. This condition can be imagined as the result of primitive connections between the main vessels being shifted into an alternating arrangement due to the pleating, so that an afferent and an efferent branch are formed; this is likely to have happened at the phylogenetic level. The first order lamellae then undergo a similar process, the pleating for the formation of the second order lamellae being much more distinct than the preceding process (Pls. 17-20); pleating can then be repeated once or twice more, so that the pinnate structure of the gill is increasingly complicated. The basic process giving the gill its characteristic structure, however, is the formation of first and second order lamellae; (Cf. Pl. 7, Fig. 4). The octopodan gill already shows marked deviations from the typical pattern at early stages, as will be shown in the chapter dealing with this group. Each first order lamella is attached to the gill axis (represented by the branchial spleen) in a way similar to the attachment of the whole gill to the mantle (Pl. 20, Fig. 3). Corresponding similarities can be seen in the higher order lamellae, although the differentiation of pleats is less distinct.

The bauplan of the cephalopod gill is strikingly different from that of other molluscan gills (placophores, gastropods) in that the efferent gill vessel lies in the medial, the afferent vessel in the lateral, edge of the gill anlage, which is otherwise typical in structure (Pl. 17, Fig. 8). This condition represents a great problem in the comparison of the respective topography of mantle cavity roofs, since it requires the assumption of certain phylogenetic modifications and morphological constructions to bridge the gap. An inevitable idea is a 180° torsion involving the base of the gill. But nothing in cephalopod development provides such a hint, and I have finally come to a different solution (Naef 1924, p. 84):

The starting point is given by the typical stages of early development (Pl. 17, Figs. 5 and 8). These stages do not show very rigid conditions regarding the direction of blood circulation (Naef 1909): At the base of the gill there is a simple blood sinus from which the lumen of the branchial heart and the large gill vessels separate slowly. In the prototype of conchifers the direction of blood circulation may have been variable, and certain conditions must then have favored an inversion in the pre-cephalopods.—It should be recalled that within the dibranchiates the octopods show strongly modified circulatory conditions in the gill; (Cf. Vol. 1, p. 666).

The key to understanding such a process is provided by the neighboring parts: The mantle sinus of the branchial area (or the Vena pallialis of the dibranchiates), which in other molluscs empties into the auricles of the heart, is connected to the afferent gill vessels in cephalopods. Ontogenetically, however, this connection is achieved rather late, as a secondary process (Naef 1909, p. 255; see also 1913, p. 400). In cephalopods this formation is once again closely associated with the gill attachment, which in turn is associated with the retractors of the cephalopodium. See the figures on pages 392, 395, 399, 418 and 422 in Naef (1913)!

Thus there is a close correlation between the strongest muscles of the peculiar (hence phylogenetically rather new) locomotory and respiratory mechanism of cephalopods (Vol. 1, pp. 83, 84, 100) and the apparently atypical circulatory conditions of the gill base, and it seems likely that this mechanism provided the driving force for the supposed modification.

The anal projection (Pl. 17) becomes more and more distinct, and its orifice is recognizable as a transverse, shallow depression. Around the latter, 4 elevations are grouped (Pl. 17, Fig. 11), giving the projection its very characteristic form: A dorsal and a ventral lip and a lateral papilla on each side of the groove. The latter grow into a pair of leaf-shaped appendages (Pls. 18-20), each with short stalk and a lanceolate broadening. On the inner side there is a longitudinal gutter. The whole complex looks like a tiny flower. Between the base of the medial edge of the gill and the anus, the renal papilla develops; its primary morphological position close to the gill base is conserved in the octopods, whereas in the decapods it is shifted towards the anus (Pl. 17, Fig. 11; Pl. 30, Fig. 7).

Several inner organs can be seen in embryos (given their transparency) after removal of the mantle; they have to be mentioned here (Pl. 17): At the base of the gills one can see the branchial hearts with their appendages, the pericardial glands.

The surrounding coelomic pouch is always distinct in decapods (Pl. 13, Fig. 3), often the base of the afferent branchial vessel, as well (Pl. 7, Fig. 4); it is not to be confused with the more laterally situated Vena pallialis lateralis which leads from the gill base to the mantle. The most lateral parts of the auricles can be seen at the base of the efferent branchial vessels; more medially situated are the Vena cava limbs with their grape-like venous appendages. They lead to the branchial hearts, and then continue into the Venae palliales posteriores, which also carry venous appendages (in their proximal part) before leaving the renal sac to finally reach the mantle. Medially between them (Pl. 7, Fig. 4) appears the posterior end of the systemic heart and the Aorta posterior, which exits the renal sac and splits into three main branches: The Arteria pallialis medialis which runs in the edge of the mantle septum to the mantle, and the Arteriae palliales laterales which join the lateral mantle veins further posteriorly.

The hindgut runs from the anal papilla posteriorly in the midline and then turns into the visceral mass. It hides only partly the large, dark or glossy inc sac, which lies in the midline as an anlage but can be shifted to an asymmetric position later (Pls. 18, 19), either to the left side (sepiolids, *Spirula*, ommastrephids) or to the right side (sepiids).—In front of the anal projection the Vena cava reaches to the middle part of the funnel gland; there it disappears from the surface aspect and splits in two. Some of its lateral branches can be seen along with the visceral nerves (Pl. 18, Fig. 4).

At the end of embryonic development the stellate ganglia show the aspect known from the adult, at least in the large-sized embryos (*Sepia*). The nerves radiate from the ganglion in stellate arrangement, slightly elevated from the inner surface of the mantle cavity. They are typical dibranchiate formations, forming the specific nerve centers of the muscular mantle and fins, in other words formations for which there are no counterparts in *Nautilus*.

7th period: The Final Growth of the Embryo and its Behavior Inside the Egg Envelopes

Muscular movements are rare and of little efficiency at early stages, up to about stage XI (Pl. 4). But the embryo nonetheless does not remain motionless in its enve-

lope. Apart from the initial pulsation of vessels, the embryo shows roughly circular movements that are reminiscent of the "rotation" of other molluscan embryos; these movements are strongly limited by the narrowness of the chorion. As there is no velum, movements are due to the short ciliation of a very large part of the epidermis, which is sufficiently powerful to generate a gliding locomotion in embryos taken from their envelope and kept in normal sea water. With some care being taken, such young embryos can be kept alive 1-2 days outside their envelopes, perhaps even longer.

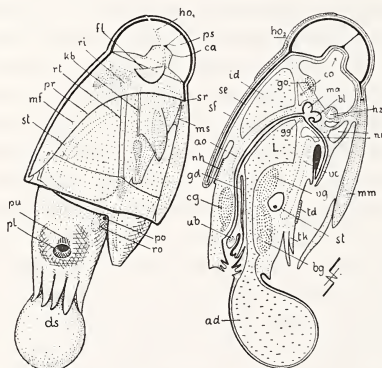
Given its weight, the yolk sac always hangs downwards (Textfig. 58) and thus takes the topographically typical position of a molluscan sole of the foot (Textfigs. 25 and 42). Long before hatching the embryo is complete in its essential parts, even though the full size and histological differentiation is not yet attained and the surface architecture is not yet smoothed out. The yolk (Pls. 19, 30) is still rather large and allows the embryo to continue growth for a considerable period inside the envelopes; during this period the organic balance (adjustment) of the parts is achieved, so that the small animal is capable of living independently under certain conditions. During this period embryos can be taken from their envelopes, or (from stage XIX) stimulated to hatch; they can then be induced to take up activities prematurely, especially those related to feeding. If the yolk sac is left with the animal (although it can be easily cut, with a minimum of loss of nutritive material), it is sooner or later dropped actively (autotomy), the navel showing strong contractions (Pl. 21). See also the final chapter.

Egg masses raised artificially, without special care, tend to release the larvae or juveniles rather prematurely. Under entirely natural conditions, the total or almost total reduction of the outer yolk sac is probably the signal for hatching to occur. In the aquarium with its rich bacterial flora, the egg envelopes are likely to be infected and disintegrated more rapidly, and the animals always leave them before they have completely resorbed the yolk sac; the latter is dropped (*Loligo*, *Sepia*) or eaten (cf. *Argonauta*).

During the final period a number of essentially secondary differentiations take place; since they are not of a general nature, they are not discussed here. The inner and outer organs function more or less normally during this period when they are stimulated: The blood circulation, which generally starts at the time of yolk sac constriction (stages in Pl. 3, Figs. 7-9), has a largely definitive layout and function. The ink sac is able to release ink, the mantle can produce the rhythmic pulsations for respiratory and locomotory movements in which the funnel takes its typical part. The suckers can adhere to the wall of the egg capsule, the eyes react to light by contracting the iris

fold, and various defensive movements can be achieved. Even without any disturbance, the embryos change their position in the chorion from time to time.

The state attained inside the egg envelopes varies greatly among groups; one organ may be more advanced in its development in relation to an other one, and the functional state is not always attained in different parts at the same stage of architectural development. Structural conditions which are clearly embryonic in some species can be attained at a larval or juvenile stage in others and then take up their functions accordingly. This raises a number of interesting problems concerning differences in embryonic and postembryonic structures and the transition from one to the other, problems that are only hinted here.



Textfigure 55. — Ideal prototype of an advanced dibrancheate embryo towards the end of intracapsular development. At the left, the animal is represented transparent; at the right a medial section (such a form can be used as a base for comparisons between all the embryonic and larval conditions of living and fossil dibrancheates. For the corresponding adult form, see Textfig. 59). — *ho*₁: Hoyle's organ (transverse branch); *fl*: fin; *ri*: insertion of funnel retractor (*rt*); *kb*: branchial band insertion; *pr*: rim of proostracum; *mf*: mantle furrow; *st*: stellate ganglion; *pu*: pupil; *pl*: primary lid; *ds*: yolk sac; *ro*: olfactory organ; *po*: pore of statocyst; *ms*: mantle septum; *sr*: shell rim; *ca*: initial cap of siphuncle; *ps*: prosiphon; *ho*₂: Hoyle's organ (medial branch); *id*: inner yolk; *se*: shell epithelium; *sf*: shell fold, enclosing the shell in a "shell sac"; *gd*: poison gland; *nh*: nuchal attachment, in contact with the "cape attachment"; *ao*: Aorta anterior; *cg*: cerebral ganglion; *ub*: lower buccal ganglion; *ad*: outer yolk sac; *bg*: brachial part of pedal ganglion; *tk*: funnel valve; *id*: funnel gland; *vg*: so-called visceral ganglion; *mm*: muscular mantle; *vc*: vena cava; *ni*: kidney sac; *hz*: heart; *bl*: caecum of the stomach (*ma*); *L*: part of inner yolk sac in the prospective position of the liver, the growing rudiment of which will progressively replace the yolk mass; *gg*: ganglion gastricum; *go*: gonad; *co*: coelom.

The medial section (at right) shows the bent neck of the yolk sac, which is typical for decapods (cf. Textfigs. 42 and 58).

140 The differences expressed at the end of the embryonic phase in the orders Octopoda and Decapoda, briefly mentioned earlier, are very profound indeed, as will be shown in detail in the special chapters. No living form in either one or the other order shows conditions that could be considered even vaguely archetypal.—To illustrate this point, Figure 9 of Plate 6 (a fairly typical decapod) and Figure 4 of Plate 30 (a fairly typical octopod) should be viewed against Textfigure 55.

141 However, all observed stages can be easily related to Textfigure 55, in which the yolk sac size can be changed at will, and in which the chambered shell can be imagined reduced or elaborated on with formation of further septa. The archetypal condition of



Textfigure 56. — Inside of mantle cavity of young cuttlefish (from Vol. 1, p. 125).

These pictures illustrate the archetypal arrangement of secondary sexual characters in a female dibranchiate; it would be rather "purely" represented, except for the ink sac (Tb) which has strongly grown posteriorly, a characteristic feature of the sepiids, and except also for the kidney paillae which have come to lie close to the anal complex, as is typical for sepioids in general. Note the wide glandular field from which the accessory nidamental glands (ac) will be formed, and the small, epithelial pouches (Nd) from which the true nidamental glands will be formed! — Left: *Sepia elegans*, 6× natural size. Right: *Sepia orbignyana*, 2× natural size, more advanced stage. — Od: oviduct (distal part); VI: Vena pallialis lateralis; kh: branchial heart; Mb: posterior limit of the mantle cavity.

a dibranchiate hatchling was probably characterized by the presence of several septa (cf. p. 79 on *Nautilus*, *Spirula* and *Sepia*);

The secondary sexual features of the female can be expressed already during embryonic development. (cf. Pl. 20, Fig. 3, nidamental gland anlagen). The same is true for the luminous glands derived from these formations (cf. Pl. 23, Fig. 9). Textfigure 56 provides a general morphological overview of these parts.

The luminous glands of sepiolids correspond to the anteriormost part of the accessory nidamental glands (Pl. 23, Fig. 9).

CHAPTER 5

The Typical Course of Embryonic Development in Decapods and Its Modification

Contents : 1. The typical decapodan ontogenesis. 2. Modification of the typical decapodan ontogenesis (p. 149)

1. The Typical Decapodan Ontogenesis

The eggs of decapods (p. 72) are always surrounded, in addition to the chorion, by secondary envelopes made of a tough jelly, which is secreted by the nidamentary glands (missing in octopods). Their morphological treatment will be presented in a future volume. The chorion is simpler; in contrast to the octopodan chorion it has no stalk-like extension at the vegetal pole (Textfigs. 18, 19); it is a simple, thin but tough membrane that is always oval in shape. The ovum itself is spherical or bird egg-shaped.

The cleavage has been described already for *Sepia* and *Loligo*, and I can confirm most of what has been stated by Vialleton (1888) and Watase (1888) (see also Köppern 1910); however, I intend to review the facts in a comprehensive, critical survey.

The decapodan cleavage shows a characteristic feature from the 8-cell stage onward (Pl. 1, Fig. 3; Pl. 13, Fig. 2) in that the lower, medial octomeres are very distinct due to their narrow form and special position, tightly applied to the symmetry plane. Their daughter cells also show a marked special aspect during subsequent

cleavage stages, and it is beyond any doubt that they take a strictly circumscribed part in the constitution of the future germ. Their nuclei do not lie in the same circle as the others; they are shifted toward the center of the blastodisc, as is the bulk of their protoplasm, so that the daughter cells will be allotted primarily to this area of the embryo.

In contrast to what might be expected, namely that the smaller cells divide more rapidly than the larger ones, the daughter cells of the posterior, medial octomeres lag behind the rest, so that from the 8-cell stage a 14-cell stage results, which is then soon completed to 16 cells. Similarly the 32-cell blastomere stage is regularly preceded by a 28-cell stage, the 64-blastomere stage by a 58-blastomere stage. (In the latter only 143 the 6 centrally located ones are retarded) This heterochrony of division between the central group of micromeres and the rest of the blastodisc remains visible for some time. But soon more complex disparities appear in both cell groups.

When the 32- and the 64-blastomere stages are achieved, the more advanced cells already show division spindles; at the 28- and 58-cell stages, signs of initial division are in turn visible in the retarded micromeres.

The 4th division step involves typically the separation of 4 micromeres from the 4 medial octomeres, whereas the others divide radially (Pl. 1, Fig. 4). In the lower octomeres this always occurs in very strict form, whereas the micromeres derived from the upper cells do not immediately give up contact with the margin of the blastodisc in *Sepia* and thus do not appear as typical micromeres (Pl. 13, Fig. 3). Similar phenomena are observable in octopods (Pl. 24). The upper octomeres also may vary with one another.

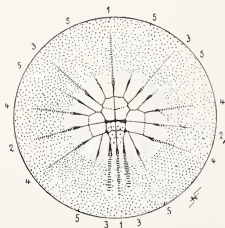
The 5th division step again shows a characteristic peculiarity, in that the two posterior, medial macromeres divide in centripetal direction and thus produce a new pair of micromeres (whereas in *Octopus* there is a radial division). While in octopods the arrangement of the micromeres varies greatly already at the 32-cell stage (Pl. 24, Fig. 12, 13), barely two germs looking exactly alike, decapods show the arrangement as in Textfigure 57 with very little variations, and the 6th division step still shows an undeniable, though less than strict, regularity (Pl. 1, Fig. 6). Only the two lateral macromeres divide radially, whereas the others give off micromeres by a more or less continuous upper and lower furrow, respectively.

The subsequent divisions occur in strongly individualized fashion, so it is impossible to reconstruct their strict course from a series of sequentially preserved stages. The individual blastomeres no longer have a strictly determined position and prospec-

tive significance. But one can nevertheless recognize as units certain cell complexes that undergo synchronous divisions; we will return to this phenomenon when dealing with *Loligo*. Thus the daughter cells of the medial posterior, especially the central plate made of small cells (Pl. 1, Figs. 6-12), can be recognized for some time; it is indeed possible to follow them (or their major part) becoming integrated into the shell epithelium, which is thus constituted essentially by these cells. The medial stripes which continue to the periphery of the germinal disc remain distinct for a long time (Pl. 1, Figs. 7-12). This is not due mainly to a special arrangement and form of the cells, but to the fact that they receive rather little material from the very beginning, so that with the method used for these observations, they always appear somewhat darker due to the yolk shining through them. Moreover, these cells continue to divide rather synchronously, but with a slight lag, so that somehow they remain distinct from the general aspect of the remaining parts of the blastodisc.

The scarcity of material allotted to these cells is probably related (as far as I can see) to the fact that the organ that will be formed from them, namely the shell, is more or less rudimentary. In *Argonauta* (Pl. 32), where this rudimentation is pushed to extremes, the position of this cell complex is taken up by a gap in the blastodisc. See also *Octopus* (Pl. 24). Something similar already is expressed in the decapods where the cell complex mentioned is not able to fill the space allotted within the blastodisc but instead shows a rather loose structure (Textfig. 57)

The result of cleavage is a roundish germinal disc, which is surrounded by a coro-



Textfigure 57. — 32-cell stage of *Loligo vulgaris*, viewed from the animal pole. 30× natural size. The numerals in the margin indicate the successive furrows formed at the corresponding cleavage steps; those furrows resulting from the 5th step that lie inside the blastodisc are indicated as dotted lines. Furrow 1 is sagittal, 2 is transversal, 3 on either side, from top to bottom, but not passing through the center, 4 again transversal (without deviation in the posterior half; deviated around the micromeres in the anterior half). The furrows of the 5th step, as far as they are not marked by dotted lines, are radial; — Note the arrangement of the 8 small daughter cells derived from the lower octomeres.

na of macromeres or yolk cells. This corona (Pl. 1, Fig. 7, 8) is not closed, however, nor is it sharply limited; in fact its elements are isolated from one another and radiate, with narrow plasmic processes, into the thin plasmic pellicle surrounding the yolk, thus producing a sun-like picture. The rays first contain one cell each; they subsequently multiply (by undergoing radial and centrifugal divisions, each group being derived from a proximal group of yolk cells) when germ layer formation begins (Pl. 1, Fig. 9).

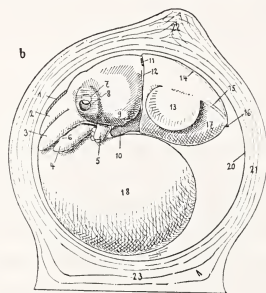
145 As already said above (p. 94) the germ layer formation consists in the transformation of the single layer of cells into a multilayered circular zone that excludes the yolk cells (Pl. 1, Figs. 8-10); it appears as a light marginal stripe in the preparations figured. Here I will not return to the analysis of the underlying process. The ectoderm shows a circular limit and it is disconnected from the epithelium of the lower layer (mesoderm) (Textfig. 31 g). The yolk cells still project as rays from underneath the germinal disc, but soon become covered by the expanding margin of the disc, along with being drawn under by their proper movement (Pl. 1, Fig. 12; Pl. 2, Fig. 1). In the course of its further growth, the ectoderm forming the "yolk envelope" leaves the light zone of the mesendoderm behind, so that a thin marginal zone of the germinal disk is formed that first comprises only ectoderm covering the yolk cells; later on a loose mesenchyme also forms. The mesendoderm subsequently becomes broader both in centripetal and centrifugal direction and thus forms a disk that is interrupted only in its center.

The cell material of the mesoderm being sorted out then begins to arrange itself in a pattern preparing the later anlagen of the external organization. This is much more distinct in the large decapods than in the octopods at my disposal, but there is no basic difference. From the beginning, in decapods (apart from the formation of 10 arm rudiments) the part corresponding to the shell epithelium is much larger in relation to the muscle mantle than in the octopods; moreover, the decapodan statocyst anlage forms a distinct patch before invagination begins. The more distinctly structured aspect can be interpreted as the expression of an actually more advanced stage that is flattened by the expansion over the yolk, by which the folding processes are mechanically hindered until growth has proceeded further. (In fact artificial reduction of the yolk mass results in accelerated folding processes.) The swelling effect of chemicals used in preparations can in turn increase the yolk volume so much that existing elevations may be artificially flattened.

The folding process enhances the achievement of a distinct pattern of organ rudiments (Pl. 2 and 15). The 10 arm rudiments may be very similar at early stages (Pl. 23), or they show more or less marked differences almost from the beginning (Pl. 6). In the latter case the tentacle rudiments present the highest rate of development, whereas the 2nd pair is never markedly retarded. Depending on the subgroup, the 3rd and 5th or the 1st pair are weaker; the 3rd and 5th arm pairs can indeed be very much retarded (oegopsids), so much so that they are formed only during postembryonic development.

The fin rudiments and Hoyle's organ always appear in typical combination on either side of the contracting shell sac porus (Pl. 2, 15).

146 Of course, the general statements made earlier (pp. 107-143) on folding processes in the germinal disc and subsequent shifts, and on embryonic elaborations, are valid for the decapods. The general rule is that the decapods reflect the typical dibranchiate development and bauplan more completely and more normally than the octopods; the latter show a more reduced bauplan due to the early degeneration of the chambered shell, the relative simplification and weakening of the swimming apparatus (lack of nuchal and funnel attachments, weak funnel retractors and muscle mantle, funnel valve absent) and the total reduction of the buccal arms; in some parts the octopods



Textfigure 58. — Embryo of *Sepietta oweniana* inside its capsule. 25× natural size. — Note the bent axis of the embryo and yolk sac, which is typical for decapods (cf. Textfigs. 20 and 55, and Pls. 6 and 19). In octopods and in decapods with a rudimentary yolk sac (oegopsids), this attitude is not observed.

1-5: arm rudiments; 6: rudimentary swimming membrane on tentacular club; 7: pupil; 8: primary lid; 9: olfactory tubercle; 10: funnel tube; 11: nuchal attachment; 12: funnel pouch; 13: fin; 14: Hoyle's organ, medial branch; 15: lateral branch; 16: terminal spine; 17: mantle sac; 18: yolk sac; 20: chorion; 21: gelatinous envelope; 22: tip of the latter, apparently formed at the end of capsule extrusion; 23: base, glued to any solid substratum.

show more simple primary features (suckers without stiffening structures, renal pore not shifted).

It is also typical for the decapod embryos that they are always, more or less markedly, bent inside the roughly globular chorion as illustrated by Textfigure 58. This position of course relates to the space limitations and some biologists might consider it even as a direct consequence in the sense of an "inheritance of acquired characters". Given the different situation in octopods (Textfig. 116) and the fact that the undeniably primary posture (Pl. 3) is the straight one in decapods, the bent attitude
147 must indeed appear as phylogenetically secondary. In any case this posture appears even without any direct effect, i.e. in embryos taken from their envelopes (or remaining inside extremely extended envelopes) (cf. concluding section).

The decapodan suckers differ from those of the octopods not only by more complex positional relationships, but also by higher degrees of structural differentiation; but these differences are externally less marked during the embryonic phase than later on, and we therefore refrain from going into the details of their morphogenesis (cf. Vol. 1, p. 662).

2. Modification of the Typical Decapodan Ontogenesis

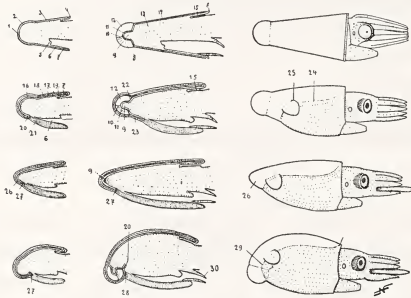
One might expect that the early embryonic stages of dibranchiates or of the decapods in particular still show a strictly uniform type. This is indeed true for many details, as shown in the preceding general description, but it is not true at all for the overall aspect. In oegopsids (see corresponding chapter), for example, the earliest organogenetic stages already show a peculiar, a typical picture, at least in outline:

One should particularly note the early expression of the interesting differences in shell form and shell insertion in the mantle sac, on which we have based our decapodan system (Vol. 1, p. 485).

Profound differences can be seen very early between the respective elaboration of a conical shell in relation to the mantle sac as expressed in the suborders Teuthoidea, Sepioidea and Belemnoidea. They are perfectly established by the end of embryonic development. This is true also for the archaic, surviving sepioids in which the phragmocone is preserved and relatively little modified (cf. Textfigs. 84-86). The teuthoids, on the other hand, show conditions (partly even in the youngest postembryonic stages)

(Textfigs. 70-73) which are strongly reminiscent of those that supposedly existed in the fossil belemnoids, as far as the formation of a partly more than hemispherical "cone" and its relation to the muscular mantle are concerned.

A similar insertion of the relatively large rudiment is observed in other teuthoid forms, at least during the embryonic phase (Pls. 8 and 9); it certainly does not generally attain the size represented by the type shown in Textfigure 71 A; but it is this maximum of cone development that should be considered primary and archetypal given its similarity to the much older belemnoids. Sometimes, however, the youngest postembryonic stages no longer show an externally recognizable cone (Textfigs. 75, 78), and even embryonic development does not produce more than an extremely modest rudiment (Textfigs. 50, 63). Indeed the gap representing the future cone within the muscular mantle can be larger than the prospective shell part actually formed in it (Pl. 10). It is generally true that the first insertion (as soon as it is histologically recognizable)

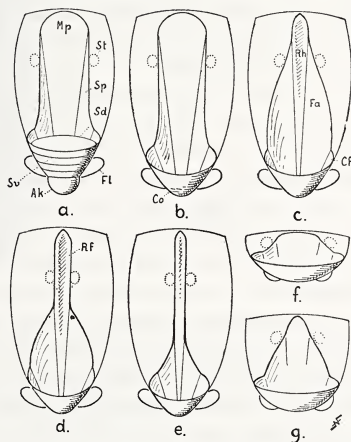


Textfigure 59. — Schematic representation of typical development of the shell and mantle sac, at three stages, in an ideal protocephalopod (tetrabranchiate, first row); in a protodibranchiate or protobelelemnoid (second row); in a teuthoid (third row); in a sepioid (fourth row). — The rear end of the teuthoid (26), i.e. the terminal cone, could have been drawn rather blunt, as illustrated in Textfigure 71 A. However, I became aware of this form only belatedly; I therefore supposed a more pronounced reduction of the cone to be generalized and characteristic for the teuthoids.

1: shell apex (primordial shell); 2: shell epithelium (matrix of mother of pearl layer); 3: dorsal shell wall (homolog of proostracum of dibranchiates); 4: mantle rim; 5: anal papilla; 6: mantle cavity; 7: membranous mantle; 8: sagittal lamella of prosiphon; 9: beginning of siphuncle; 10: main pillar of prosiphon; 11: initial cap of shell siphuncle; 12: initial chamber; 13: visceral sac; 14: shell epithelium; 15: nuchal attachment; 16: cone portion of embryonic shell; 17: proostracum portion of embryonic shell; 18: shell fold; 19: outer (secondary) and inner (primary) shell epithelium; 20: ventral rim of phragmocone, penetrating into the visceral sac; 21: muscular mantle; 22: first septum; 23: ventral wall of phragmocone; 24: rim of proostracum, with insertion of the muscular mantle; 25: fin; 26: cone; 27: position of primary insertion of the muscular mantle; 28: secondary insertion of the muscular mantle; 29: secondary insertion on outside of the phragmocone; 30: funnel tube.

of the muscle mantle in the cone area is again on the rim of the shell or shell sac (vol. 1, Fig. 203).

The decapodan proostracum also shows important differences providing the basis for our classification of teuthoids, namely the subdivision into Pro-, Meso- and



Textfigure 60. — Diagrams illustrating the shell insertion in the mantle sac (represented as transparent) in belemnoids and teuthoids, and visualizing the modification of the proostracum in teuthoids (cf. Vol. 1, p. 162).

- a) Belemnoid at an early stage (advanced embryo); reconstructed (cf. Textfigs. 55 and 28).
 b) Prototeuthoid (same conditions). Proostracum still broad, belemnoid-like; often considered as belemnoid shells when found in fossil beds (cf. Naef, 1922, pp. 108, 109, 169).
 c) Mesoteuthoid, with narrow, gutter-shaped medial plate or "rachis" (Rh) and broad lateral wings (Fa) or "vane" (loc. cit., p. 148).
 d) Metateuthoid, with anteriorly "free", vaneless rachis (Rf), allowing the stellate ganglia to lie close together, and imposing a very narrow shape on the nuchal attachment (Vol. 1, p. 146).
 e) Extreme variant of the metateuthoid type; exists as typical form in cranchiids, chiroteuthids and brachioteuthids (Vol. 1, pp. 236 and 371). But see also the ommatostrephids (Vol. 1, p. 412).
 f) Early embryonic condition of c, d and e, still reminiscent of b and a in having a broad rudiment of the proostracum.
 g) More advanced embryonic stage, with narrowing rachis (cf. Pls. 8 and 9). At this stage the shell can be represented by the empty shell sac, or even by a simple gap in the muscular mantle.

Mp: medial plate of the proostracum; St: stellate ganglia; Sp: lateral plate of the proostracum; Sd: dorsal part of the latest suture (4th septum); Sv: ventral part of the latest suture; Ak: initial chamber; Fl: fin; Co: cone (conotheca of the rudimentary phragmocone); Rh: rachis (condensed, bent medial plate); Fa: vane (broadened lateral plate); Cf: cone vane (continuation of the vane by the dorsal cone wall); Rf: free rachis.

Metateuthoidea. Although we know from direct observation (Naef 1922) only adult (fossile) Proto- and Mesoteuthoidea, their comparative study allows us to obtain a picture of their typical features during embryonic development (Textfig. 60 b, c). An important guide is the similarity between the oldest teuthoid group and the belemnoids, on the one hand, and the archetypal character of the teuthoids in general regarding the connection between shell and muscle mantle, on the other hand; and finally, starting from the fossil, the stepwise approach to recent forms as illustrated by the known developmental and biological aspects.

The oldest teuthoids (cf. Naef 1922) were indeed quite different from the extant and younger fossil types. In particular it should be recalled that the shells of most prototeuthoids and some mesoteuthoids were more or less heavily calcified, so that they were heavy and unflexible, suggesting a *Sepia*-like life form rather than a squid-like aspect. These animals were at least partly benthic (primary mode), a specification to the diagnosis given in volume 1 (p. 235). This probably had its developmental counterpart: I suppose that their embryos were similar to those of *Sepia* in terms of size and external morphology. However, the proostracum anlage must have been more similar to the situation observed in the oegopsids figured in Plate 8, Figure 4 and Plate 9, Figure 9, where the shell sac (or the dorsal gap of the muscle mantle in which the shell should normally lie—see also under *Octopus* and *Argonauta*, and the following volume) is rather broad in the beginning and becomes progressively pointed only later, as is typical for the meso- and finally metateuthoids.

This typical modification, which is reminiscent of a recapitulation of ancestral stages, could be even more pronounced in the oegopsid species illustrated in Textfigure 71 A, and the earliest anlage could indeed have a more markedly belemnoid and prototeuthoid aspect. Here it is interesting that even at postembryonic stages this form has a proostracum surprisingly similar to the shell of the fossil *Beloteuthis acuta* (vol. 1, Fig. 62), i.e. of a typical mesoteuthoid. Textfigure 71 B shows an animal with not only metateuthoid features, but with the much more narrowed (degenerated) vane typical for the brachio- and chiroteuthoids and the cranchiids. Textfigure 61 shows the insertion of a rather normal metateuthoid shell with a rudimentary cone in the mantle sac.

Atypical features in this picture are the outline of the fins, the total reduction of the cone, the bridge-like passage of the gill attachment and Vena lateralis pallii (VI) from the body to the mantle, and a certain secondary extension of the shell rim on the

inner surface of the mantle sac which somewhat obscures the archetypal structure of the metateuthoid shell. The normal state is illustrated in Textfigure 62.

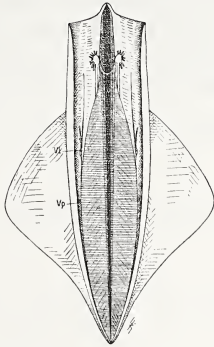


Fig. 61.

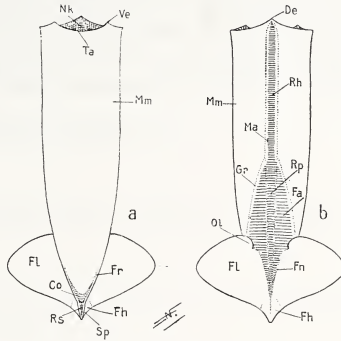


Fig. 62.

Textfigures 61 and 62. — Correlation of mantle sac, shell and fins in the metateuthoids.

Textfigure 61. — Preparation of a female *Loligo vulgaris*, $1/2\times$ natural size (from Vol. 1, p. 169; see also pp. 185 and 200 of Vol. 1, with figures representing the same specimen). The ventral half of the mantle sac is cut away, the viscera are removed. One recognizes the gladius, the muscular mantle, the fins, the stellate ganglia with the posteriorly departing fin nerves, the posterior (Vp) and lateral (Vi) mantle veins and the gill insertions.

Textfigure 62. — Mantle sac, shell and fins of metateuthoids in archetypal shape and arrangement (cf. Vol. 1, p. 153). Ventral view at left, dorsal view of mantle (represented as partly transparent) at right. Note the outline of the mantle sac and of the mantle rim, and of the fins, and reconstruct the aspect of the shell.

Nk: nuchal attachment; Ta: funnel bay; Ve: ventral mantle corner; De: dorsal mantle corner; Mm: muscular mantle; FL: fin; Fr: free shell rim, ventral; Co: cone; Rs: rostrum; Fh: fin membrane; Sp: body tip; Rh: free rachis; Ma: muscular mantle insertion on gladius; Rp: posterior, embedded part of rachis; Fa: lateral vane; Ol: "earlobe"; Fn: fin insertion (articulation).

In the sepioids one can again notice that more ancient belemnoid prototype features are present to widely variable extents. In *Spirula* and its fossil relatives a transitional stage of the mantle sac similar to Textfigure 71 A is likely; it is indeed not surprising that Joubin took this animal for a young *Spirula*. The homologous stages of *Sepia* and *Sepiola* (Textfigs. 89 and 100) are so thoroughly modified that they need to be discussed separately. To visualize the typical situation, one will have to use

151 Textfigure 30 (p. 88) and the hypothetically completed Textfigure 86, as long as the

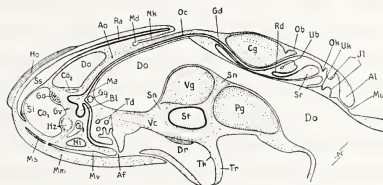
true *Spirula* stages are not known. It is to be hoped that they will be discovered soon, since we now know something about the frequency and distribution of this “living fossil” (vol. 1, p. 863). New insight into the typical shell and mantle development can also be expected from *Idiosepius* (Textfig. 87), the general habit of which is certainly closer to the archetype of the suborder than are the spirulids, sepiids and sepiolids, and the anatomy of which also shows some archaic features (see also Chapter 8 on sepioids)

CHAPTER 6

The Embryonic Development of the Loliginids

Contents: 1. Generalities, 2. *Loligo vulgaris* (p. 156), 3. *Loligo forbesi* (p. 175), 4. *Loligo pealei* (p. 175), 5. *Alloteuthis media* (p. 175), 6. *Septoteuthis* (p. 177).

1. Generalities



Textfigure 63. — Medial section of an advanced embryonic stage of *Loligo vulgaris*, slightly schematic (from Vol. 1, p. 187); About 30× natural size; — cf. stage XV in Plate 6, Figure 6, and Textfigures 50 and 55. Here we see the typical overall organization of a dibranchiate embryo. However, the cone part of the shell sac is already almost non-existent (cf. Textfig. 60), the position of the siphuncle (Si) barely recognizable. The whole organ is sharply divided into the parts containing the vane and the rachis, respectively.

Ho: Hoyle's organ (medial part); Ss: shell sac; Go: gonad rudiment; Si: siphuncle rudiment; C₁, 2, 3: coelom sections; Gv: genital vein; Hz: heart; Ms: mantle septum; Mm: muscular mantle; Mv: ventral mantle cavity; Af: anus; Ni: kidney; Do: yolk; Ma: stomach; Gg: Ganglion gastricum; Bl: caecum; Td: ink gland; Vc: Vena cava; Tr: funnel gland; Tk: funnel valve (rudiment); Tr: funnel tube; St: statocyst; Sn: blood sinus; Vg: visceral ganglion; Pg: pedal ganglion; Cg: cerebral ganglion; Sr: subradular organ; Ao: anterior aorta; Ra: rachis part of shell sac; Md: dorsal mantle cavity; Nk: nuchal attachment; Oe: oesophagus; Gd: poison gland; Rd: radula pouch; Ob: upper buccal ganglion; Ub: lower buccal ganglion; Ok: upper beak; Uk: lower beak; Il: inner lip; Al: outer lip; Mu: mouth.

Among the known dibranchiates and especially decapods, the loliginids probably are closest to the archetypal ontogenesis, as far as the overall aspect is concerned. They are so suitable as examples for general orientation that we used them repeatedly in Chapters 3 and 4.

Of all the forms available to me (*Loligo vulgaris*, *Loligo forbesi*, *Alloteuthis media*, *Alloteuthis subulata*) I have studied and figured *L. vulgaris* in greatest detail; but I had also access to most developmental stages of the other species. There are no essential differences, so I refrain almost totally from treating these species, emphasizing their great similarity at the outset.

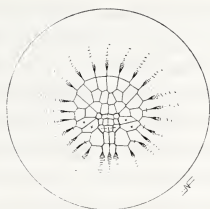
2. *Loligo vulgaris*

The newly laid eggs of this species (as in all other decapods studied) are still immature; the formative yolk is concentrated centrally at the posterior pole. The normal eggs, which are available in Naples from spring through summer (they are often laid by animals in the aquarium), measure 2.2 mm in length and 1.6 mm in width. This size is variable, however: the enormously large animals sometimes captured have somewhat larger eggs in several gradations stored in their oviducts. Eggs brought in from the field that measure more than 3 mm in length are probably those of *Loligo forbesi*, because they show remarkable differences in their inner organogenetic differentiations. About 6 hours after spawning, maturation and spreading of the blastodisc are completed and the first cleavage division can be observed (Pl. 1, Fig. 1), followed by the second and third cleavage divisions, each after another hour. After about 24 hours cleavage is complete and germ layer formation begins (Pl. 1, Fig. 8).

Cleavage divisions generally occur very regularly, as figured in Plate 1; at the 64-cell stage deviations from the norm are still minor, and therefore it is easy to spot them.

Perhaps a whole egg mass shows variations in detailed aspects, as in the case of one in which all the eggs showed the cleavage pattern of Text figure 64. Other peculiarities also were recognizable. These eggs developed into perfectly normal advanced stages.

Due to the delayed cleavage pace of the posterior medial octomeres, the 16-cell stage is briefly preceded by a 14-cell stage, the 32-cell stage by a 28-cell stage, and the 64-cell stage by a 58-cell stage (p. 145). The age of the respective developmental



Textfigure 64. — 64-blastomere stage of *Loligo vulgaris*. The cells marked × show an abnormal (but frequently occurring) position. See Plate I, Figure 6!

154 stages can be determined only approximately from the outset. Since the sperm cells have to cross thick gelatinous layers presenting variable local conditions, fertilization does not take place simultaneously in all eggs within a collective capsule, so that the eggs differ in their respective developmental stages due to these variations. An egg taken from such a capsule does not tell much about the other eggs; for a precise picture of developmental progress it is indispensable to preserve individual egg samples in addition to observing the live eggs, at least during the early stages. During later development the conditions (e.g. oxygenation) may again differ for individual eggs within a collective capsule, so that one always finds some embryos that develop more quickly and others that lag behind. Moreover, the different capsules of a large egg mass are not deposited at exactly the same moment, so the actual age of an individual embryo is practically always unknown.

Generally one egg mass does not allow one to observe the entire development, since under normal aquarium conditions infections and ensuing perturbations of development are inevitable. Thus one will observe the different phases of development on different egg masses under not quite identical temperature conditions. The speed of embryonic development varies greatly indeed with the water temperature. The developmental times indicated therefore are only approximations, and for other species I have largely or entirely refrained from giving such indications (cf. p. 90). The figures of the plates are drawn essentially after specimens from two egg masses; the early stages up to 6 days in early April, the more advanced stages from eggs laid in mid-July. In the latter season, the developmental phase covering 6 days in spring would take only about 3.5 days. But I was never able to make parallel observations on these

early stages on a large egg mass in summer, and I was also unable to obtain very late stages of perfect quality from an egg mass received in April.

We begin with our observations on the course of cleavage by using Plate 1.

At the time when the first cleavage furrow can be observed, one finds a peculiar, radially arranged concentration of the protoplasm lying outside the blastodisc; it will disappear later on. The cleavage furrow broadens towards the periphery of the blastodisc and encroaches upon the neighboring part of the egg surface, but only for a short distance. The subsequent radial furrows show the same conduct. After the first cleavage step the blastodisc appears slightly extended bilaterally in an oval shape; subsequently it returns to a roughly circular outline.

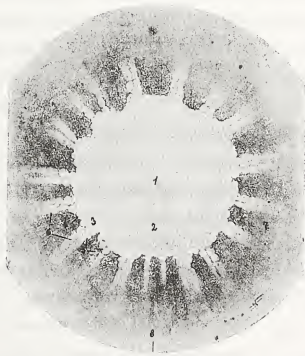
The second, transverse furrow shows no peculiarity; it presents the typical arrangement (p. 93) with incomplete separation of two upper, somewhat larger blastomeres having obtuse angles in the blastodisc center, and two lower, smaller blastomeres with acute angles. The third furrow produces the typical 8 blastomere stage of decapods, the medial, posterior octomeres being distinct in both their shape and position. Their upper parts, which are shifted to the center of the blastodisc, generally join the other cleavage cells rather tightly, but some, more or less clearly defined gaps may appear, as in *Sepia* embryos. The nuclei are distinctly shifted towards the center.

During the fourth cleavage step the first four micromeres are formed in typical fashion; the upper two are markedly larger than the lower two and are always cleaved off completely (in contrast to *Sepia*).

They divide during the fifth cleavage step by a transverse furrow in the upper two micromeres and by sagittal furrows in the lower two, while the two lateral macromeres next to the second furrow give off large new micromeres; the lower medial ones give off smaller micromeres, and the remaining cells divide radially. Thus the typical 32-cell stage of decapods is attained (p. 146).

The sixth cleavage step, as a general rule, has its furrows inserting at right angles to the preceding ones. Therefore all the macromeres that have not given off a micromere during the preceding step, generate micromeres, whereas the other four, lateral macromeres divide radially. Likewise the micromeres generally behave in the same way (but see Textfig. 64). An exception are the posterior medial macromeres, since they again give off micromeres, and the lateral micromeres, which divide once more radially. The result of these cleavage steps is shown in Plate 1, Fig. 6. A slightly older stage is shown in Plate 1, Fig. 7. It still presents the general arrangement of the 64-cell stage,

and it is indeed easy to identify the central group of cells derived from D, and the further descendency of D cells. In the marginal zone a modification appears which has started during the preceding stage: the macromeres move radially away from one another; the furrows reaching beyond the blastodisc broaden and turn indistinct. This process continues to the end of cleavage, just before the superposition of marginal cells begins; only narrow strips of protoplasm derived from loosely clustered marginal cells can then be observed (Textfig. 65). These marginal cells are arranged in 16 to 20 small groups; for each of these generally two strips radiate out from corresponding cells. They sit in corners which project from the margin of the blastodisc, their cells showing an intermediary aspect between the yolk cells and the other elements; later on they come to lie under the margin of the blastodisc. They probably represent the endodermal cell material. In general this stage and the following ones (Plate 1, Figs. 9-11) show two delicate rays which are weaker than others and only in single file. These are the remains of the D macromeres; their identity is often demonstrated by the presence of a somewhat darker strip of cells reaching towards the generally also darker center of the blastodisc, where the majority of the micromeres derived from D should be located.



Textfigure 65. — Germinal disc of *Loligo vulgaris* at the end of the cleavage process. 50× natural size.

Note the enlarged marginal cells (3, 4), which are distinguishable due to their lighter coloration, the projecting corners (5) and the rays (6) joining them, starting out from the yolk cells. Note especially the two lower strips (derived from the D macromeres) and the neighboring stripes (5) leading to the central part (1) of the blastomere.

156 Quite often this whole group of cells is distinct due to a particularly marked furrow separating it from the rest of the blastoderm, even though this demarcation seems rather insufficient for any morphological conclusion.

Germ layer formation now begins by a superposition of cells in the marginal part of the blastodisc which thus shows several layers of cells. In contrast to the sepiids and sepiolids, this process (which will not be analysed here in detail) does not occur simultaneously all around the periphery of the blastodisc; it is concentrated (much like in *Octopus* 'Plate 24, Fig. 17') in distinct corners of the blastodisc margin, between which the unilayered condition persists (Plate 1, Fig. 7). A particularly large gap appears ventromedially, in a position corresponding to the D macromere. The D octants thus are not involved, in the formation of the mesendoderm, at least not from the beginning. This peculiarity is still recognizable when the clearly demarcated ectoderm (Plate 1, Fig. 9) begins to grow over the mesendoderm and the yolk cells (Plate 1, Fig. 11). But these parts of the germ soon unite to form a solid ring, which remains interrupted only medioventrally; this gap later grows into a simply weaker spot (Plate 1, Figs. 10-12). This spot is always associated with the two delicate yolk rays derived from the D octants, which allow one to orientate the blastodisc.

157 Once the endodermal ring is formed, the outline of the blastodisc tends to become circular, except for the yolk cell rays, the outer parts of which are still visible. The majority of the latter now appear as single rays, but in greater numbers, and persist for some time in this typical arrangement (Plate 1, Fig. 12), later to be retracted definitively under the margin of the blastodisc (Plate 2, Fig. 1). This margin is rather delicate, generally unilayered (Cf. p. 104) so that the position of the yolk cells underneath is recognizable. Meanwhile the mesendoderm grows in surface and follows the advancing margin of the germinal disc; towards the central part the mesendoderm ring broadens so that the darker, unilayered central part (p. 105) grows ever smaller. Finally it takes up the approximate position of the central D descendants, which—as a formerly distinct group—disappear from the surface aspect (Plate 2, Fig. 2). But the spot remains recognizable (due to the persistence of the unilayered dark zone) for a sufficiently long period to reveal the shell fold as a peripheral formation (Plate 2, Figs. 4-6). This demonstrates the derivation of the shell epithelium as an anlage from the central cellular plate (Plate 1, Figs. 6-12) derived from those peculiar D octants. In gastropods the anlage of the shell epithelium is formed by a similarly positioned complex of cells derived from the posterior (in this case unpaired) so-called D macromere.

Incidentally the mesendoderm ring shows a more or less distinct segmentation long before it spreads throughout the cellular territory representing the prospective embryo proper. The ventromedial gap remains partly visible and generates a distinct indentation of the embryo anlage (Plate 2, Figs. 1-3), in front of which the otherwise closed ring shows a clearly weaker spot. Soon afterwards, however, this situation is inverted in that a cell concentration appears (Plate 2, Figs. 3, 4) where the gap was; its morphological significance is already clear: it is the anlage of the hindgut, which forms a cellular plate at this stage; in contrast to the assumptions of Korschelt (1892) and Teichmann (1903), this plate does not represent the entire gut anlage (midgut rudiment without the ectodermic foregut), since the latter is much wider laterally (though not yet entirely epithelial at this stage in *Loligo*):

Close to this spot the mesendodermal ring already shows early on an enhanced inner marginal zone (Pl. 2, Figs. 1-3), which later becomes broader. This zone contains mainly the material for the muscular mantle (Pl. 2, Figs. 4-6). Finally the mesoderm closes in circular contraction beneath the shell epithelium, later than what it achieved in similar fashion at the opposite end, close to the edge of the germinal disc (Pl. 2, Fig. 3), where it formed a thin layer accompanying the "yolk envelope" and thus participated in the establishment of the yolk sac. Thus the outer limit of the light zone that later proves to represent the body of the animal is not a persistent, sharp border line that could hinder the centripetal advance of the inner germ layer.

158 In germinal discs only 4 days old (Pl. 4, Fig. 3), parts of the prospective embryo can be distinguished: Around the dark central gap, the mantle rudiment forms a still poorly demarcated ring. Medially behind it, a light spot marks the hindgut. The edge of the light zone essentially represents the arm crown position, except for the anterior part in which the mouth rudiment appears. On either side a foggy cell concentration is visible in anterior position; they are separated from one another in the midline by a dark zone. Later on, they will become recognizable as the cephalic anlage containing especially the eye (au) material. One day later (Pl. 2, Fig. 4) this part is already more clearly demarcated, much like the other parts: In the mantle rudiment the shell fold shows up as a light and dark border line, and the free mantle edge also is visible. Below it is on either side a light patch representing the paired gill rudiments along with material for the visceral ganglia (similarly, the cerebral ganglia are included in the cephalic anlage, and the pedal ganglia are part of the arm crown rudiment, from which they become detached due to ectodermal cell immigration.) The arm crown (foot) is also distinct, especially in its lower (ventral) parts.

The yolk is now covered for more than one-half and will soon become entirely enclosed (Pl. 8). After one more day (Pl. 2, Fig. 5) the germinal layer is ready to undergo folding processes. The lay-out of the cell material allows one to recognize already the arrangement of the major anlagen. Only about 1/4 of the yolk mass is still uncovered by the embryo, which forms a sort of envelope similar to the shell of a hard-boiled egg, from which the top has been removed (Cf. Pl. 26).

Of the arm rudiments (other than the rudimentary medial one marked x) two are distinct on either side (IV, V): They correspond to the ventral arms and tentacles. A third rudiment (III) is less distinct, and the two dorsal arm pairs (I, II) are represented by a blurred, narrow strip encircling the germinal disk and coming to an end on either side of the mouth. These arm rudiments are not individually visible; on the whole the arm crown at these stages appears rather continuous, as a unit from which the individual arms become differentiated as secondary formations, in a way probably reminiscent of the phylogenetic process.

The funnel tube rudiments (tr) are faintly recognizable as very narrow, turbid strips, whereas the cephalic anlage with the eyes (au) and the anteriorly and medially situated buccal indentation (mu), the mantle rudiment (ma), the gill rudiments (km), the site of the anal papilla (an) are recognizable in their typical form. The statocysts (st) show up as light patches situated in a sharply delimited, dark, angular field, distinct from both the cephalic anlage and the funnel pouch rudiment. The latter grades typically into the strip surrounding the gill rudiments, which has been identified as the anlagen of the parietal strands (p. 104). They are still rather indistinct, but in a preparation they show up more clearly than the funnel tube rudiments (a fact which is not revealed perfectly in the reproduction of my drawing, the funnel tube rudiments appearing too distinct).

Above the mantle rudiment, in a position corresponding to the nuchal cartilage (nk), one sees a dark zone and a small dark spot lying inside the shell epithelium, which remains recognizable during the subsequent stages; it is probably formed during the closure of the centripetally advancing mesoderm but has no special morphological significance. It could be considered as the rudiment of a "shell gland" similar to other conchiferans (see Textfigure p. 61), but one should realize that the shell epithelium here is already spread out, so that the shell gland would have to be flattened out. (Either this formation is a speciality of the heteroneurans 'cf. pp. 47, 60' or the cephalopods, being good conchiferans, had it and then lost it early on during their

phylogenetic development or at the transition from the tetrabranchiate form to the dibranchiates. Only the embryo of *Nautilus* could give some information.)

Less than 24 hours later, all these anlagen become very distinct elevations and depressions: the folding of germ surfaces indeed starts (Pl. 2, Figs. 6-7 and Pl. 3, Figs. 1-3). By that time the yolk generally is entirely enclosed. The shell fold and the eye folds appear, and the posterior (prospectively upper) edge of the mouth, the anlagen of the statocysts and the cephalic mass, the funnel pouches, the mantle rim, the gills and arms form low yet distinct elevations. Soon after that (Pl. 2, Fig. 7) the eyes and the shell folds begin to contract, whereas the edges of the mouth and the statocysts follow somewhat later. Among the arm rudiments, the three dorsal pairs become increasingly distinct, the second and third being differentiated from the hitherto rather compact piece of arm crown lying close to the statocyst, whereas the first (dorsal) arm pair arises from the part lying close to the eye, which is the last part to become enhanced. Thus the establishment of the 5 pairs of arm rudiments is not uniform, neither in terms of the time of first appearance nor with respect to the primary spacing in the arm crown or the primary extent of their elevation. The two ventral arm pairs develop in advance, the others follow; the dorsolateral and ventrolateral arms (II and III) arise from an anlage that appears as one structure for a rather long time; once they are distinct they stay close to one another, whereas the dorsal one arises in a markedly isolated position—an isolation that remains visible for a rather long time (Cf. Pl. 3).

As far as the size of the rudiments is concerned, that of the tentacle grows fastest, as is generally the case in decapods, whereas the dorsolateral arm rudiment lags behind. If one had to define an arm formula based on the stage shown in Figure 8 of Plate 2 (the arms being ranked according to their size, the arm numbers used corresponding to their order from top to bottom, as indicated in Vol. 1, p. 115), that ranking would be (with the tentacles included as number 4 among the arms): 4, 2, 5 = 1, 3, a situation which obtains also for *Sepia* and probably represents the archetypal situation. Clearly, from this state the third arm pair has the greatest chances to lag even further behind, to a lesser extent arm pairs 5 and 1.

All of these three arm rudiments indeed can be clearly rudimentary in certain forms and developmental stages of decapods, a situation which is probably so marked due partly to intrinsic developmental conditions, partly to special adaptational relationships.

In the course of another two days, starting from the stage shown in Figure 7 of Plate 2, most of the folding process will be achieved (Figs. 8-12). The arm crown contracts (Pl. 3) and by this constriction separates the embryo proper, whose rear end points upwards, from the yolk sac; the eye vesicles close, and around the point of closure the iris fold arises. Swollen elevations appear on the cephalic anlage; they correspond to the different elements of the white body, which are separated by typically arranged furrows that appear in homologous positions also in *Sepia* and *Sepioloa*. The edge of the mouth contracts once the rudiment of the poison gland is invaginated in the central part of the buccal complex; in the vicinity of this invagination the rudiments of the subradular organ form swollen elevations. The funnel folds rise to form the funnel flaps and unite with the funnel pouches. The statocysts become closed. The fin rudiments and Hoyle's organ appear on the mantle anlage on either side of the point of shell sac closure, while the gills and the anal papillae are pulled underneath the mantle edge.

This development, viewed in morphological orientation, is represented by the subsequent Plates 3 and 4, in three different views for each embryo—the only way to provide a complete picture. (It should be noted that the stage VIII shown in Figures 1-3 of Plate 3 appears unnaturally globular due to the swollen yolk mass; in life it would be somewhat more slender, with a more distinct surface sculpture. Subsequent stages are also drawn from preserved specimens, but with an attempt to render the natural form more closely.) Let us now consider the stages in their natural sequence.

Stage VIII (Cf. Pl. 2, Fig. 6) shows a general change of overall form, similar to what Watase (Korschelt and Heider, 1909, general part, volume 3, p. 136) described for the egg of *Loligo pealei*, in contrast to what appears in the younger stages. The "egg" drawn by Watase is an advanced embryo rather than an egg or cleavage stage, as demonstrated by the faintly illustrated distribution of germ material. Therefore the orientation of younger stages cannot be found according to this bilateral egg shape; it is indeed necessary to study very carefully the germinal disc itself, as has been shown in our earlier sections (Cf. also Lang, 1900, p. 445).

The embryonic body is now markedly compressed in dorsoventral direction, as if a mechanical pressure were acting on the anal area. Thus in particular the distance
161 between the mantle edge and the arm crown has strongly increased along the ventromedial line (Cf. Pl. 26), a phenomenon that we have interpreted in phylogenetic terms (pp. 115-118).

The embryo proper now surrounds about one half the yolk, sometimes a little more (Cf. Textfig. 69, with embryos of *Alloteuthis*) and appears demarcated from the yolk sac by the arm crown, in which all five arm pairs are clearly recognizable. The arm crown is separated from the cephalic part by a sharp furrow, which appears in similar stages of all dibranchiate embryos and which proceeds in ventral direction between the funnel anlage and the arms, without being continuous ventrally. Similar but less marked furrows delimit the anlagen of the cephalic complex, the statocysts, the gills, the mantle and the funnel pouches from one another. It is striking that the bottom of the shell sac does not form a depression; it bulges up as a hill rising above the shell fold. Similarly, the retina does not represent an "eye pit" but is a convex surface (even in life) except for the peripheral parts already covered by the eye fold. The mechanical cause for this phenomenon lies in the yolk mass which is under the pressure of the enclosing tissues. A ventral view shows, in addition to the changes already mentioned, several remarkable details (platefigures* 27, 30, 33, 36):

In the platefigure 26 note the individual parts of the arm crown, among which the medial one is still distinctly visible; on either side of it the rudiments of the ventral arms and those of the tentacles follow. Laterally a diffuse formation is visible from which both the second and the third arm arises; on the left side of the body these arms already appear distinct. Behind the arm crown a sharp furrow delimits the lateral parts of the cephalic anlage from the arm crown and, more medially, from the funnel tube rudiments. The latter are still continuous with the arm crown medially; this is one of the reasons for which I consider the funnel as derived from the arm complex. The latter should be taken as the actual homolog of the molluscan foot. Behind the funnel tube, and still more distinctly visible than the latter, one finds the transverse connection lying between the funnel pouch rudiments (p. 106).

At stage IX (Pl. 3, Figs. 4-6; cf. Pl. 2, Fig 8b) the dorsoventral flattening of the embryo becomes even more distinct, and the contraction of the arm crown, which provides the starting condition for the constriction of the yolk, can no longer go unnoticed. The individual arms have become more or less prominent knobs. The eyes have completely closed, and the statocysts have halfway closed their pores; the buccal

*Scientific Editor: Naef uses here a different numbering of figures, which does not correspond to the published system (perhaps he forgot to eliminate it from his manuscript); he probably alludes to Figures 2, 5 and 8 of Plate 3 and Figure 2 of Plate 4 (whereas "platefigure 26" at the beginning of the following paragraph indicates the lateral view in Figure 1 of Plate 3).

invagination is in a similar state, the originally anteriorly situated depression of the poison gland rudiment being shifted slightly backwards, while the swollen elevation surrounding it represents the anlage of the subradular organ. The cephalic anlage shows the swollen parts of the white body, separated by shallow furrows, arranged around the eye; on either side of the mouth the cerebral ganglia are recognizable. The mantle cavity now starts to form a depression on the dorsal side as well.

162 The ventral aspect reveals elevated funnel tube folds (funnel lobes); they are not yet connected (medially from the statocysts) with the funnel pouches, but they are now more distinct than the medial connection between the funnel pouch rudiments (p. 106); this medial connection is now rather indistinct and restricted to a pair of low elevations preserved as light patches (td) lying behind the funnel lobes. We can already recognize them as the funnel glandanlagen. Behind them is the anal projection, which already shows a slight elevation; on either side of it lie the gill rudiments forming low humps. On the upper surface of the cap-shaped mantle sac, the half-closed shell fold forms a slight elevation, which foreshadows (x) the later formation of the fins.

At stage X (Pl. 3, Figs. 7-9; cf. Pl. 2, Fig. 10) all these structures have become more marked: the fin rudiments are really distinct, the surface of the anal projection shows a slight depression indicating the future opening. The gill rudiments are more robust and are shifted beneath the mantle; the statocysts are nearly closed; the funnel folds are slightly curved inwards, and the mouth invagination is deepened. Especially the constriction of the yolk has strongly progressed, and the arm rudiments now form robust warts, whereas the ventral rudiment (x) is much less visible in the arm crown. The embryo body as a whole has contracted, and the eye stalks are now beginning to form as very large, obtuse humps.

At stage XI (Pl. 4, Figs. 1-3; cf. Pl. 2, Fig. 12) the constriction of the yolk is essentially achieved. (But see also Textfigure 42) The arms begin to differentiate: the first suckers become visible as flat elevations. In a posterior direction the arm pillars form round papillae; however, they are really distinct only on the inner two dorsal arm pairs (Pl. 4, Fig. 3). Those of the third arm pair join closely those of the second arm pair, while the pillars of the ventral arms join closely those of the tentacles; the latter now start to grow strongly in length and each already shows 3 sucker rudiments in single file.

The rudiments of the funnel tube are now more strongly curved towards one another and are connected to the similarly elevated rudiments of the funnel pouch, which can be viewed in relation to the submersion of the statocysts at the angle of connection. The statocysts are almost completely closed, leaving only a faintly visible

pore (St) at the surface. The funnel retractor rudiments form delicate stripes reaching towards the mantle pouch; inside the prospective funnel tube cavity the funnel gland becomes increasingly distinct.

The cephalic section shows the eye stalks at the peak of their development, and in the eye proper the iris fold appears as a flat circular ridge (ir); on either side a deeper furrow separates an anterior from a posterior section of the apical field. The latter is surrounded by the swollen parts of the white body (ka). The mouth is very narrow and lies on a low elevation wedged between the dorsal arm pillars, which represents the slowly disappearing conchiferan snout.

163 The mantle sac is more strongly convex and the fin rudiments elevated. The aspect from behind (above) shows the shell sac to be completely closed, and the typical inverted T-shaped scar which radiates from the point of closure forms the axial figure of the fin rudiments, as in Text figure 37 on page 111 (Pl. 2, Fig. 12).

Figures 4-6 of Plate 4 show some transitional states. They represent different degrees of advance in the further development of the mantle cavity and the formation of the funnel tube up to the fusion of the vault-like funnel lobes. This fusion starts at the tip and rapidly progresses in the posterior direction. Along with the ensuing establishment of the funnel apparatus the outer statocyst pores disappear.

Stage XII shows the cephalopod body established in its essential parts, and the inner organization reaches a state on which morphological considerations can be suitably based. Indeed the muscular mantle, the fins, the funnel lobe fusion, the number of gills, the thickened eye stalks (p. 114), the closed eye chamber, the iris fold, and the reduced number of arms already show the dibranchiate features in great clarity. However, the embryo is still far from reaching the state of a viable, free juvenile, so again one may wonder whether an earlier cephalopod stage of tetrabranchiate nature has already ceased to be expressed here.

Certainly this is not the case since the original arrangement of the parts, i.e. the gross bauplan, is the general cephalopodan heritage, and the relationships between brachial apparatus, head and eyes, funnel apparatus and mantle pouch must be the same in the tetrabranchiates (cf. Textfig. 25). But this is not true with the finer proportions: according to general knowledge, the simpler sense organs of tetrabranchiates should be expected to take up a lesser mass of anlage tissue; conversely the more complicated shell apparatus should be accelerated in development. This assumption provides the base for our attempt to construct an embryonic form for the *Nautilus* organization (Textfig. 25).

How little of the tetrabranchiate features are recapitulated in *Loligo* is easily understandable to the careful reader. We can find only the recapitulation of *embryonic* states of ancestors, some conservative ones, some more advanced, but everything aims at generating the real organization of an extant loliginid.

The arm crown is now even more strongly contracted, the suckers, especially those of the tentacles, have grown into hemispherical warts. The arm pillars reach backwards over the head dorsally and ventrally; the apical part of the head is more distinctly structured than in the preceding stage. Instead of the furrow mentioned there (Pl. 2) a broad window (fe) is now visible; its significance will be dealt with in the anatomical section. Due to a slight upward bending of the rear end, the broadly rectangular, obliquely flattened shape of the eye stalks and the form of the fin area appear very clearly in Figure 9 of Plate 4. The shell sac scar is accompanied by light stripes, which represent the anlage of Hoyle's organ (s, n₁).

The mantle cavity has grown markedly deeper, and the gills would nearly disappear in it if they had not grown in length in their turn. Each of them forms a slightly flattened papilla on which a transverse furrow on either side (i.e. dorsally and ventrally) indicates the formation of a first gill filament. The latter is nearly or totally basal, subsequent filaments being formed more distally with further growth of the tip.

At stage XIII (Pl. 5, Figs. 1-2; Pl. 6, Fig. 4) the formation of the arms and cephalic pillars has made progress: those of the first arm pair (pf₁) have spread on the head surface and are no longer distinctly recognizable. But they are not confluent with those of the two neighboring arms; they continue to be individualized. The posterior parts of the second and third arm pillars (b) have approached the eye, the edge of the third arm pillar being directed toward the eye. A similar situation is observed in the ventral pillars; the ventral edge (vk) belonging to the tentacle pillar is at a greater distance from the eye, however.

Progress has also been made by the posterior funnel edge and the mantle rim, which are preparing to establish definitive relationships: the funnel pouches are already slightly inserted below the mantle rim, the posterior edge of the funnel tube approaches the mantle rim and is more complete than at stage XII, especially in the transition to the funnel pouches. The area of the nuchal attachment (nk) begins to become distinct. The gills and the anal projection lie deep in the mantle cavity and disappear almost entirely from the surface aspect. On the arms and on the mantle the first dark (here still yellow-brownish) chromatophores appear. At this stage the mouth is

just visible from above, but it is reduced to a small pore; it begins to be overgrown by the dorsal arms.

Stage XIV is shown in Figures 3 and 4 of Plate 5 (note that the figure numbers 5 and 6 on the plate are erroneous) and in Figure 5 of Plate 6; at this stage an overall modification of the head starts in that the eye stalks are slowly drawn in, so that the typically larval head shape progressively appears. The eyes themselves become directed more and more anteriorly, so that they come to lie in a position anterior to the tissue masses derived from the eye stalks. While this shift begins, the ocular edge of the arm pillars reaches backwards past the eye proper, especially on the dorsal side. As usual the ventral side again lags markedly behind the dorsal side; on the latter a delicate skin fold appears close to the posterior end of the eye; it will subsequently form the "posterior connecting piece" of the primary lid fold (p. 124). At this stage, it does not yet reach the ventral edge of the eye, however.

The sucker rudiments of the arms have grown into nearly globular papillae; they begin to arrange themselves in four rows on the tentacles, whereas for the rest a zigzag arrangement becomes generalized, the earliest sucker rudiments being already shifted away from the medial axis of the arm.

The posterior edge of the funnel is already inserted in the mantle, the funnel tube seam is completely closed, and the typical form of the embryonic mantle and fins is achieved. The fin shape is reminiscent of fossil teuthoids (Naef 1922, p. 114) and can be considered as typical for the entire suborder. With a direct development, this should become a transversally drawn out lobe with a very distinct lateral corner. This corner is already recognizable, and it remains visible during subsequent stages (Pls. 5-7), but later disappears to be replaced by the typical juvenile fin of metateuthoids (Textfig. 62*). In certain preparations, the dorsal side of the mantle is sufficiently translucent to show the gladius, the general outline of which also exhibits the typical metateuthoidan form; but (in contrast to the oegopsids) its conus is very rudimentary from the earliest stages onward (cf. Textfigs. 63 and 71).

The already narrow, long free "rachis" of the juvenile gladius is particularly noteworthy; it is typical for all the Metateuthoidea. As far as can be seen from the outside, it no longer expresses an older condition characterized by a broad middle plate (cf. Textfig. 60*), which is transient as an early rudiment (Stage X). At this and subsequent

*Scientific Editor: erroneously given as Textfig. 49 and Textfig. 2 in original text.

stages, the stellate ganglia can be seen close to each other through the dorsal mantle surface. (cf. Vol. 1, p. 146).

The free mantle rim already shows the three typical corners, which are found in all teuthoids, namely a strongly projecting, dorso-medial one and two ventral ones which flank the shallow indentation for the funnel.

Stage XV continues in the same direction (Pl. 5, Figs. 5, 6 'erroneously labeled as 3 and 4 on the original plate' and Pl. 6, Fig. 6). The primary lid fold is underway to become closed: the ventral head covers are now strongly extended laterally, and they are connected by an inconspicuous gutter (x) to the slight fold mentioned earlier (i.e. the "posterior connecting piece" of the lid fold). This gutter marks the site which has to be covered by the posterior end of the lid edge (v) before it reaches the connecting piece (Cf. Pl. 6, Fig. 6).

The ventral side of the head, behind the eye, shows the beginning contraction and separation of a large part of the preserved primary epithelium; this flat, oval elevation occupies the lower side of the formation called the "cheek-hump". The mantle sac and the head begin to grow elongate; the number of chromatophores continues to increase.



Stage XVI shows an embryo with a fully established primary lid (or corneal) fold (Pl. 5, Fig. 7; Pl. 6, Fig. 7; a slightly more advanced stage is given in Textfig. 66). This condition has been brought about by the progression of the lid edge of the ventral head cover along the path described above, to the point where it met the posterior connecting piece to fuse with it (Cf. Pl. 6, Figs. 6 and 7). For a very short period of time, one can distinguish the heterogeneous components of the annular fold in *Loligo*; it is marked by a delicate indentation representing the point of fusion (Textfig. 66).

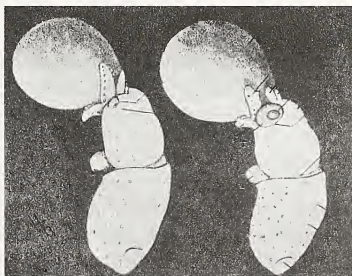
The formation of the anterior connecting piece of the lid fold is difficult to observe in undissected embryos of *Loligo*. This part is of morphological interest, since it provides the

Textfigure 66. — Embryo of *Loligo vulgaris*. 20× natural size. Stage XVI. Note the freshly formed lid fold (5), especially the point of fusion (13) between the edge of the arm pillar and the posterior connecting piece, and the general outline of the fully formed embryo which is typical for decapods. — 1: yolk sac; 2: tentacular arm; 3: ventral arm; 4: eye ball; 5: primary lid; 6: olfactory tubercle; 7: cheek hump; 8: mantle sac; 9: fin; 10: chromatophore; 11: funnel tube; 12: prospective funnel opening (still closed).

location where the lid pore is finally closed. Phylogenetically this probably has passed through an intermediate state similar to the definitive condition shown more or less clearly by the larger oegopsids (cf. Vol. 1, Fig. p. 110 and p. 446); the widely open primary lid of these animals indeed shows an anterior indentation ("sinus") in a corresponding position (vol. 1, p. 115). In *Loligo* a similar, but transient formation is sometimes recognizable.

The formation and subsequent closure of the lid fold places the eye ball inside an orbital chamber and pulls it more closely than before towards the median plane; thus the prominent eye stalk condition is brought to an end. For some time (Textfig. 67; Pl. 5, Figs. 8, 9; Pl. 6, Fig. 8) a condition persists that permits a fairly wide opening when the lid fold is relaxed, whereas its contraction restricts the opening to a small pore surrounded by a wrinkled edge. The latter state is finally adopted definitively (Pl. 5, Fig. 9; Pl. 6, Fig. 9). In the meantime several other surface differentiations appear: the olfactory tubercle becomes more distinct (Pl. 5, Figs. 8, 10), the mantle sac becomes stretched longitudinally while the yolk sac decreases in size; the funnel shows its adductors more distinctly (Pl. 5, Fig. 10). First signs announce the formation of a "funnel locking apparatus", i.e. nuchal and funnel attachments become recognizable; but a really distinct, functional form will be achieved only later (Pl. 7).

The final stages XVII-XIX of embryonic development are characterized by a strong size increase, especially in the longitudinal axis, while the outer yolk sac is



Textfigure 67. — Embryos of *Loligo vulgaris*. 26× natural size.

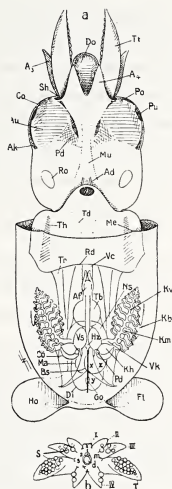
a) Stage XVI-XVII. b) Stage XVII-XVIII. Note contraction of the lid fold (7, 17) over the eye ball.

1. yolk sac; 2. tentacular arm; 3. dorsolateral arm; 4. dorsal arm; 5. iris; 6. position of the buccal mass; 7. primary lid; 8. funnel pouch; 9. nuchal attachment; 10. stellate ganglion; 11. chromatophore; 12. fin; 13. ventral arm; 14. eye ball; 15. olfactory tubercle; 16. funnel tube; 17. orbital pore; 18. pupil, visible through the integument.

167 rapidly, reduced, partially by utilization of the nutritive material, partially by active transfer of the yolk mass to the inner yolk organ. The general proportions thus undergo changes that are obvious to an observer comparing Plates 5-7: the head gets its definitive form, the tentacles begin to grow out after a developmental stagnation during which they had not grown beyond the condition of short stumps; the mantle sac grows not only in absolute but also in relative size and attains the capacity to perform abundant swimming movements long before hatching (around stage XVII); these movements serve inside the egg capsule to change the position of the animal.—The most conspicuous transformation is visible in the fins: the lateral corner disappears and is replaced by a broadly rounded rim. This gives the fins their spatular form, which can be observed in all young teuthoids.

The brachial apparatus already shows the essential features of the earliest postembryonic stages, and the striking differences in the respective sizes correspond (since stage XIV) to the definitive arm formula (cf. Vol. 1, p. 175). The arms of the first pair are still papilla-shaped rudiments (Textfig. 68b), each of which will form a small sucker rudiment only shortly before hatching. The arms of the second pair have two small, but distinct sucker rudiments, those of the third pair four, and those of the fourth pair again two; all arms have an additional, less distinct sucker rudiment. Only the tentacles, which still show a very short stalk, are more strongly developed and have a greater
168 number of suckers (mostly non-functional) arranged in 4 rows. All arms have a pointed tip, which represents the terminal growth bud. Between the arm bases and the buccal zone, the earliest, indistinct rudiments of the buccal pillars can be seen to form delicate papillae in close connection with the proximal parts of the arms (Textfig. 68 b, 1-4). They continue to develop only during the postembryonic phase.

Stage XX, i.e. the mature juvenile form of Plate 7 (cf. Textfig. 68) requires a detailed inspection. There is still a small yolk sac, since egg masses kept in an aquarium always release the larvae before the total reduction of the outer yolk sac, in contrast to what happens under fully natural conditions without any outside disturbance. This is demonstrated by occasionally collected egg masses containing fully developed embryos. If the yolk sac has become very small (no larger than in the figure), it is fully resorbed during the first two days following hatching, or it is eaten by the young animal (cf. *Argonauta*). If the yolk sac is larger than that shown in the figure, it is autotomized and sinks to the bottom of the tank. The ultimate yolk sac remainder is strongly wrinkled; it consists of the shrunken envelope of the former food reserve.



Textfigure 68. — a) Newly hatched *Loligo vulgaris*, 18X natural size. — Drawn after living individual, which is entirely transparent; figure finished based on the preserved specimen. From Volume 1, page 188.

b) Arm crown of an embryo at stage XVIII, after removal of the yolk sac (situated at d). The mouth (m) lies above the yolk scar. The sucker rudiments (s) are not yet numerous; they are lacking altogether on the rudimentary (retarded), stub-like dorsal arms. The rudiments of the buccal lappets (1-4) are barely visible as minute, flat papillae. 1-4: arms; r: tentacular arms.

The main figure (a) shows the remaining, small yolk sac (Do) between the arms; the small, stub-like, pointed arms (A_3 , A_4), beyond which the tentacles extend; the web fold (Sh) between the 3rd and 4th arm which defines the (still shallow) tentacle pouch; the eye balls (Au) in the closed orbital chamber (Ak, hatched); its pore (Po); the cornea (Co); the olfactory tubercles (Ro), which are differentiated as flattened pads on the ventral side of the head; the funnel adductors (Ad); the funnel complex with the newly-formed funnel attachments (Th) and the ventral parts of the funnel gland (Td, visible through the funnel tissue); The anal pailla (Af); the Vena cava (Vc); the hindgut and ink sac (Tb); the funnel retractors (Tr); the gills with the alternating gill lamellae on either side, the branchial spleen (Km), the branchial band (Kb) which is still limited to the proximal part of the organ; the branchial heart (Kh) with its appendages (Pd); the sac-like branches of the Vena cava (Vs) which receive (from behind) the Venae palliales posteriores (z); the Aorta posterior (x) and its bifurcation into the Arteria pallialis medialis and the Arteria pallialis posterior (y); the rounded, laterally extending fins (Fl) through which the lateral branches of Hoyle's organ (Ho) are visible (dotted lines); etc. — Go: gonad rudiment; Di: inner yolk sac; Bs: caecum; Ma: stomach; Cö: coelomic pouches containing the branchial hearts; Vk: auricle of the heart; Hz: heart chamber; Kv: branchial vein; Ns: kidney sac; Rd: posterior edge of the funnel tube; Me: ventral mantle corner; Mu: superficial, straight cephalic muscle; Pd: ocular stalk inside the orbital chamber.

Along with the small mouth, the underlying yolk sac stalk occupies the position of the prospective mouth; it is surrounded by the 10 arms, which show the typically unequal development (p. 163); they are strikingly feeble compared to the body of the animal, as is the rule in the youngest larvae of the teuthoids and octopods, in contrast to the sepoids. Swimming membranes are entirely lacking; only the ventral arms show a distinct edge on the outside. It grades proximally into the rib-like rudiment of an umbrellar elevation that surrounds the tentacle base, which in turn is slightly lowered and thus prepares the formation of the future tentacle pouch (Textfig. 68a, Sh).

The eye region can be understood from its earlier history: compare, one after the other, the figures on Plates 5 and 6. The eye balls, each of which had been sitting on a stalk, now project (from a remainder of the stalk) into a cavity, inside of which it retains some mobility. This "orbit" communicates through a very delicate pore with the surrounding medium; but normally this pore is so tightly closed that it is not easily detectable; the orbital wall is stretched by the fluid pressure built up in the cavity. The pore crosses the corneal fold obliquely; subsequently a sort of ball-valve forms inside the fold. The eye balls proper show some modifications: an outer lens segment begins to form, which however remains smaller than the inner segment, and the iris fold adjacent to the outer segment is no longer circular, since its upper edge is now forming a typical iris lobe (Pl. 7, Fig. 5).

The shape of the head has reached the typical juvenile metateuthoid condition: it represents roughly a rectangular plate, the anterior corners of which are occupied by the eyes. The posterior corners are represented by the "cheeks", which are shaped
 169 mainly by the enclosed white bodies; their ventral side carries the oval olfactory tubercles, which are now more contracted than before.

The fully functional funnel apparatus (Pl. 7) has a typical dorsal "nuchal attachment", an elongate plate (nk) with sharp edges, which adheres to the apposed mantle. The funnel attachments are still poorly demarcated (Fig. 4). But their general form, which is typical for young teuthoids, is recognizable (cf. Vol. 1, Pl. 3, Fig. 4; Pl. 4, Figs. 1 and 2). Inside the funnel tube lie the funnel valve and the funnel gland.

The general outline of the mantle sac of course depends strongly on the state of contraction; accordingly it may appear slender or rather plump. Its margin shows the three typical corners which already appeared at earlier stages (XIV, XV). On the upper side of the posterior end, are the prominent strips of glandular epithelium forming the anchor-shaped organ of Hoyle. Its lateral branches reach over to the fin surface on each side while the medial part forms a transverse rib, which extends beyond the mantle sac apex

and forms a connection between the fins. The latter are truly terminal and their union at the posterior end, which is typical for the loliginids, is now underway (but see also Pl. 8). This union is probably related to the atrophy of the conus (p. 168, Textfigs. 60-62).

The embryonic development of the organs of the mantle cavity does not show any atypical peculiarities, so the fully formed juvenile fully formed juvenile shows a condition that can be considered typical for such stages in decapods, especially in teuthoids (Pl. 7, Fig. 4; Textfig. 68).

3. *Loligo forbesi*

I consider that the strikingly large egg masses occasionally obtained from greater depths, which contain ova measuring more than 3 mm in length (Jatta, 1896, Pl. 7, Fig. 1) belong to this species. Surface development of the embryos is essentially similar to *Loligo vulgaris*, so the above description is valid except for absolute sizes and developmental speed. The embryos and homologous juvenile stages are roughly 50% larger than those of *Loligo vulgaris* (cf. p. 71).

4. *Loligo pealei*

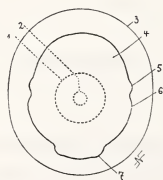
The American form, which is doubtless more remote, does not differ much from
170 *Loligo vulgaris* either, as far as can be judged from the descriptions by Watase, Brooke and Verrill. However, these data and figures are not sufficiently detailed for a thorough comparison.

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5. *Alloteuthis media*

Eggs of this species are available year round, though not in great numbers, in the Gulf of Naples (Jatta, 1896, Pl. 7, Fig. 16); apart from the capsule shape and egg

size (p. 71), they are very similar to those of *Loligo vulgaris*. The youngest as well as the older embryos look the same as those described above; they are simply smaller and more delicate. In contrast, the intermediate stages (VIII-IX) show a peculiar feature reminiscent of oegopsid embryos (Textfig. 69). Indeed the embryonic body encloses a strikingly large portion of the nutritive yolk; the yolk sac, which will later show the typical constriction, is markedly smaller than in normal embryos of *Loligo vulgaris*.



Textfigure 69. — Living embryo of *Alloteuthis media* at stage VIII-IX. 20× natural size. Outline drawing as seen from above. In the center, the apical view of the mantle rudiment is added for comparison (dotted lines, semi-schematic). Note size relation between the yolk sac and the anlage of the embryo proper (cf. Pl. 3).

1: mantle rim; 2: shell fold, surrounding and progressively covering the primary shell epithelium; 3: chorion; 4: yolk sac, here oegopsid-like, relatively small and still poorly demarcated; 5: arm rudiment (lateroventral arm); 6: eye; 7: mantle rim, only beginning to rise.

Even in *Loligo vulgaris*, the embryonic anlage initially surrounds the greater part of the nutritive yolk (Pl. 3, Figs. 1-3), and it is only later that the yolk is extruded in a hernia-like sac; but in the present species this situation is much more pronounced, as shown in the above figure. At later stages, however, the embryo proper contracts rapidly and thus generates a yolk sac almost as sizable as in *Loligo vulgaris*. Only in abnormal development do loliginid embryos, as far as I have observed, occasionally retain the primary positional relations: the yolk then is largely enclosed in the embryo proper so that its body is strikingly deformed and expanded. This produces forms which will be later considered from the point of view of developmental mechanics, but they are also interesting for systematics, because they are so close to normal oegopsid development, which appears more like a deviation.

6. *Sepioteuthis*

Wülker (1913, Pl. 22) has figured some developmental stages that clearly belong to this genus. If his figures are correct, then *Sepioteuthis* shows a remarkable difference in the formation of the embryonic and larval fins: they are completely separate in the median line and seem to lack the typical relationship (p. 168) with Hoyle's organ (Fig. 2a). I certainly doubt the latter, especially since Wülker has totally overlooked this organ in a newly hatched animal (Fig. 2c). Even in the sepiolids with their very atypically shifted fins (Pl. 23, Figs. 4 and 7), this primary correlation is clearly conserved.

CHAPTER 7

The Embryonic Development of the Oegopsids

Contents: 1. Generalities. 2. The embryonic development of the oegopsid X (p. 189). 3. The embryonic development of the ommatostrephid Y (p. 192).

1. Generalities

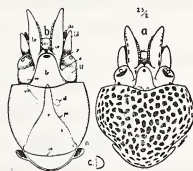
Our knowledge about the embryonic development of oegopsids, the group containing the majority of living cephalopod genera, is still extremely incomplete. This definitely modern, diversified group of decapods of generally nektonic to pelagic habit (cf. p. 152) shows related particular features in spawning, which are unfortunately difficult to observe. As far as is known, the oegopsids lay their eggs (surrounded by gelatinous envelopes, as in decapods in general) in large, floating masses, which generally remain offshore and at certain depths; they appear to be carried up to the sea surface or near the shore only rarely.

The first such egg mass was described and figured by Quoy and Gaimard (1830, p. 472, Pl. 14B, Figs. 1-4). It was cylindrical, measured 3 feet in length and contained thousands of eggs arranged in single file inside strings of the same gelatinous material as the common jelly mass.

Similar (?the same?) egg masses are reported by d'Orbigny 1839 (Ferussac and d'Orbigny, 1839 under "*Octopus membranaceus*", *Octopus*, Pl. 28, Fig. 4),
173 Collingwood 1870, Grenacher 1874 (cf. Tryon, 1879, Pl. 20) and Nishikawa 1906. A

fine description of a series of stages with detailed figures was given by Grenacher (cf. Textfig. 71 below). The data and drawings provided by Nishikawa have the advantage that they relate to a correctly identified species, *Abraliopsis scintillans* Berry*, which is widely distributed in Japanese waters, occurs in great abundance and is fairly well understood in its ecology. The other egg masses cannot be identified to species; even the embryos so carefully studied by Grenacher cannot be assigned to a family, let alone to a genus or species.

The same is true for the first egg mass, the embryos of which are described here



Textfigure 70. — Grenacher's oegopsid embryo at hatching. 12× natural size.

a) Ventral view drawn after the original figure (Grenacher, 1870, Pl. 40, Fig. 12) of a strongly contracted animal. Note the widely separate, semicircular fins entirely visible from the ventral side (cf. Textfigs. 55, 71, 72). Note also the numerous, densely set chromatophores, the retarded ventral arms (ve) and the lack of lateroventral arms, and the rudimentary yolk sac (do); ld: laterodorsal arms.

b) Reconstruction of the animal, with outlines likely to exist in the living animal, with a transparent mantle sac and a broad shell cone. (About this sort of reconstruction, see Vol. 1, p. 305, and below, Textfigs. 73, 75 and 79).

as the oegopsid X; this could be *Calliteuthis*, *Histioteuthis*, or *Thysanoteuthis*, since there is one species from each of these genera in the Naples area.

The second egg mass described here is from an ommastrephid, most probably *Stenoteuthis bartrami*; a third one, which is very similar, could be from *Ommastrephes sagittatus*.

Needless to say, there is absolutely no doubt that these embryos are from oegopsids; this is demonstrated by a number of distinct, striking features that are rather atypical for decapods.

The oegopsids strongly deviate in their embryology from all the other decapods, indeed from the dibranchiates in general, and therefore they deserve special attention. This attention is not so much concerned with the generally typical features, since these metateuthoids indeed lie far from that type, but with the observation and interpretation

*Scientific Editor: now *Watasenia scintillans*.

74 of specific features. It should be remembered that in chapter 2 some peculiarities already were mentioned that make oegopsid stages assist in understanding the general bases of decapod organization; this is especially true for the topographical relationships between mantle and shell, which demonstrate so clearly the relations of teuthoids and belemnoids. In contrast, the overall features of advanced embryos, especially the lack of a true yolk sac and the peculiar reduction of the embryonic brachial apparatus into three pairs, are rather secondary modifications derived from the typical developmental course. In this respect the oegopsids certainly cannot be considered as "primitive" forms, as is often done; the same is true for the whole anatomy. It is even conceivable that the open primary lid could be due to a secondary inhibition of its formation. See the concluding chapter.

The eggs of the oegopsids generally are smaller than those of other decapods, and during embryonic development they show certain phenomena resulting from a reduced yolk content. Their shape is almost globular and thus contrasts with the loliginids and other decapods in general; it contrasts in an even more pronounced manner compared to the octopods.

The cleavage and germ layer formation has never been studied in detail; drawings in my possession suggest that the yolk mass is fully enclosed in the yolk envelope already at very early stages, which results in a rough topographic deviation rather than in a fine-grained morphological modification of the typical development.

The relative reduction of the yolk mass (which is correlated with an increase in egg numbers, similar to what occurs in the pelagic groups among the octopods) of course alters the mechanical conditions for the achievement of organ formation: the trend towards a complete enclosure of the nutritive mass here meets a lesser resistance, and thus leads to a more complete success, compared to the other embryos in which the same trend is visible at early stages (p. 176) but then fails given the insurmountable obstacle; at the same time, however, the result of a process has thus been shifted forward which typically occurs much later in decapod development (p. 171). The embryonic body of normal dibranchiates (Cf. Pl. 3), once it has reached the stage shown in Textfigure 69, begins to turn rather solid and to contract, as if striving to achieve the positional relationships of the organs according to the body plan. It is only then that the yolk organ, which forms the obstacle, is extruded in a hernia-like extension, the typical yolk sac thus being formed. (See also Pls. 32, 33). In contrast, in the oegopsid embryo the yolk is enveloped almost completely at an early stage already,

thus maintaining the body surface under strong tension until the yolk is absorbed; the yolk cannot be extruded since the arm crown, which lies beyond the egg equator, is already contracted. (See also Textfig. 69 and Pl. 9, Fig. 5 for comparison).



Textfigure 71. — An early larval oegopsid from the Balearic Islands (cf. Joubin, 1920, Pl. 11, Figs. 8 and 9, and Vol. 1, p. 393). Note the typically retarded lateroventral (l) and ventral arms (v), the large funnel (i), the barrel-shaped muscular mantle (inserted at the shell rim x), the strongly developed, almost belemnoid cone (c) with the proostracum (p) and superficially added fins (f); see also Textfigures 55, 59 and Plate 8, Figures 7 and 8.

A) Dorsal aspect of the mantle. The proostracum is tentatively completed by asymptotic lines, to indicate the division into parts corresponding to the rachis (r) and lateral plates (s). g: stellate ganglion.

B) An early cranchiid stage (cf. Vol. 1, p. 393), in ventral view. — d: yolk sac remainder.

B₁) Dorsal view of B.

Both larvae show the very conspicuous cone of juvenile oegopsids, which led both Joubin and myself to misidentify them first as early stages of *Spirula*. The mantle sac shows the picture constructed for typical decapodan dibranchiate stages (cf. Textfig. 55), which is also valid for *Spirula* (Textfig. 86). Neither Joubin nor I had realized that early stages of typical teuthoids (oegopsids) may show such a huge cone that could be considered the rudiment of a (conceivably functional) initial chamber; it is only with the present work that the relations between the shell rudiment and the muscular mantle become clear.

The juvenile shown in A almost could be taken for the larva of a surviving belemnite; however, the anteriorly pointed proostracum (similar to *Beloteuthis acuta* (cf. Textfig. 60 c) indicates an obvious metateuthoid trait, and the arm crown permits the safe identification of an oegopsid: the 3rd and 5th arm is stub-like, inhibited in its development; the head is typically teuthoid. We could be dealing here with a chiroteuthid or a cranchiid; in these groups the cone is often very large at the adult stage (Vol. 1, Textfig. 193); or perhaps it is a *Pyroteuthis* (cf. Textfig. 73).

175 This counterbalancing of opposite dynamic conditions in the embryo should be amenable to experimental control. (See the concluding section). In such experiments, two methods might allow myopsid embryos (*Loligo*) to mimick the oegopsid condition:

a) reduction of the contracting tension in the germ during the stages following the early maximum of yolk enclosure (Textfig. 69), b) reduction of the yolk mass.

The processes of mesoderm concentration preparing the surface organization (Pl. 176 9) and the onset of surface folding are not yet known in detail; my own material does not allow me to make any definitive statement on these processes.

My description therefore begins only with stage VIII (Pl. 8, Figs. 1-2), which corresponds roughly to *Loligo* embryos of that stage (Pl. 3). At first sight a tremendous difference appears in the topographical arrangement of the organ anlagen: the oegopsid embryo gives the impression of a very strongly contracted yolk envelope having dragged an elastic embryo to cover the yolk. The mantle rudiment appears particularly extended; in contrast to the disc- or cap-shaped mantle rudiment of other embryos at that stage, the oegopsid mantle rudiment is bowl-shaped and encloses a considerable portion of the inner yolk organ. The mantle rudiment thus appears clearly organized, in a partially primary and a partially secondary manner, which emphasizes the arrangement of the parts, especially of the muscular mantle and the shell complex.

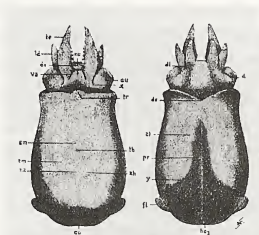
A light, ring-shaped zone, the anlage of the muscular mantle, can be distinguished from a darker, thinner zone, the shell area, through which the yolk is visible. In contrast to e.g. *Loligo* (Pl. 3), where the shell sac is still widely open, the shell fold already is closing over the shell sac bottom. This is the expression of a peculiar heterochrony in that the formation of the shell sac anlage of oegopsids is accelerated. This is made possible at least partly by the apparent retention of a sufficient rudiment of the original shell conus.

The overall picture of the later development is, of course, altered due to the fact that the entire complex of organ rudiments is stretched out over the yolk organ, the embryo remaining very strongly extended. Effects of this condition can be seen up to the establishment of the typical larval body and nearly total resorption of the maternal nutritive reserve, after which almost *Loligo*-like conditions are achieved. This can be visualized by comparison of Textfigures 68 with Textfigures 71, 73-80. This situation can be seen more markedly in special details, and it would appear even more striking if appropriate stages were available from a really complete series of material.

The course of individual ontogeneses should be viewed also in relation to postembryonic stages that can be compared with the most advanced embryos of *Loligo*. One of the peculiar features of oegopsid development related to reduction of the yolk mass is the fact that the young animals hatch from the egg mass at a stage showing relatively low differentiation, with only the most vital organs being "prematurely" completed to

become functional. The small animal shown in Textfig. 76, which is so reminiscent of very young *Loligo*, has already passed a certain time in free "larval life", as can be surmised by analogy with the development of *Abrialiopsis scintillans*; the same can be said for Textfigure 77.

It is not surprising therefore to find considerable heterochronies in oegopsid development in comparison to normal decapod development, although individual rudiments and resulting organs develop according to the same pattern: the arms, the mouth, the statocysts, the eyes, the funnel tube, the funnel pouches, the gills, the anal papilla, the muscular mantle, Hoyle's organ and the fins go through stages very similar to those of *Loligo*.



Textfigure 72. — Newly-hatched juvenile stage of the oegopsid X, the development of which is partly figured in Plate 8 (from Vol. 1, p. 161). (About identification of this animal see below, page 189)

The primary lid fold is not yet formed (the points d and x would have to be connected by a delicate fold behind the eye. The huge, scoop-shaped cone (Co) is very conspicuous; it appears as a dark membrane (visible through the integument) and surrounds the posterior end of the body, carrying the small lateral fins (f). Anteriorly and dorsally, it grades into a narrow proostracum (pr), on either side of which the stellate ganglia (s) are recognizable. ho2: lateral branch of Hoyle's organ; y: insertion of the muscular mantle on the gladius; hz: heart; km: gill; an: anus; tb: ink sac; kh: branchial heart (organs visible through the mantle); tr: funnel; au: eye; va: ventral arm; do: outer yolk sac (rudimentary); ld: laterodorsal arm; te: tentacle; mu: mouth; dl: glandular ridge. 20× natural size.

The arms first show up as papillae in a uniform ring-shaped anlage, which dorsally comes to lie anteriorly to the mouth (Pl. 8, Fig. 2; Pl. 9, Fig. 6). A very important feature is the apparent lack of two pairs of rudiments, which are in fact inhibited; they are the ones corresponding to arm pairs 3 and 5 of other decapods. Thus, in oegopsids only the two mediodorsal arm pairs and the tentacles are distinct from the beginning, whereas the other two pairs sometimes appear only during postembryonic development. In comparison to the sepiolid condition, in which ten arms appear simultaneously and uniformly (Pl. 23), which can be considered the primary condition, the

peculiar mode of oegopsid arm development can be viewed as an extreme case of heterochrony. It should be remembered, however, that even in *Loligo*, the arms are not formed in a strictly uniform fashion (p. 159), and that the arm rudiments corresponding to the temporarily missing arms of oegopsids are rather frail in the beginning (Pl. 2, Fig. 8). What is particularly striking is that the inhibited rudiments, especially the
 178 third arm rudiments, will later have a special significance and will in general become the strongest arms.

The mouth becomes surrounded by the dorsal arm bases in a way similar to what happens in *Loligo* and thus gets to lie inside the arm crown. The statocysts (Pl. 9) become distinct somewhat later, but they do not show any notable peculiarity. The eye rudiments are even less special than are the eyes proper. However, the strong expansion of the area surrounding each eye on the yolk surface reduces the prominence of the eye stalks, which are merely hump-shaped elevations of the head. Later on, a situation very similar to that observed in *Loligo* will nevertheless ensue (Textfigs. 76-77).

The formation of the funnel apparatus is achieved in the typical fashion, whereas the invagination of the organs of the mantle cavity appears somewhat retarded. The gills take a papillar form only later and even in the mature embryo they are extremely rudimentary, with only 2-5 gill lamellae each.

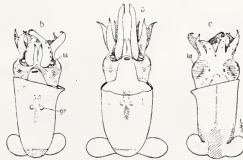
The muscular mantle has a belt-like position from the beginning; it then forms a fold forward except in the retarded mediodorsal zone; it thus surrounds an annular, slit-like mantle cavity (Pl. 9). Hoyle's organ and the fin rudiments show a development similar to *Loligo* (compare Pl. 2, Figs. 11 and 12 with Pl. 12, Fig. 3). The general bauplan of the young animal (Pl. 4) thus becomes visible much earlier than in *Loligo* or *Sepia*; in general terms the development is more direct than what can be surmised for the archetypal cephalopods. One has to remember, however, that the newly-hatched animals generally are very small (1-3 mm) and in many respects incomplete (arm crown, gills, eye lids), which makes them really appear as larvae, and that they attain, by heterochrony, the organizational level of a young *Loligo* only after a rather long neкто-planktonic life in the open water (Textfigs. 72-80).

The arm crown of the youngest larvae not only lacks arms 3 and 4*, the two dorsal pairs and the tentacles are very poorly developed; they are short and frail. The ten-

*Scientific Editor: Naef here uses the "usual" numbering of arms, which excludes the tentacles from the series; what is here called "4" is the ventral arm, the same as "5" in the earlier statement (p. 177) about the rudiments "corresponding to arm pairs 3 and 5 of other decapods".

tacular clubs each bear a small number (4-10) of suckers arranged in only two rows, the 4 sessile arms have only one each. The more advanced embryos show a relationship between the muscular mantle and the gladius that is of high morphological significance (Pl. 8, Figs. 7 and 8; Pl. 10, Figs. 1-3). The muscular mantle represents a plate bent into a cylinder, the edges of the plate becoming fused only at the anterior end, whereas the rest leaves a gap of increasing width posteriorly; this gap appears darker due to the transparency of the non-muscular tissue (through which the yolk mass is visible) and contains those parts of the embryonic shell sac and shell that correspond to the belemnoid proostracum (Textfig. 60 g). The latter grades posteriorly into the more or less scoop-shaped cone that is reminiscent of the initial chamber rudiment of a belemnoid (Textfig. 55); this part closes the posterior gap of the mantle sac. The formation of a solid shell in this part can be greatly retarded while the corresponding gap grows smaller (Pl. 10; cf. also *Octopus* and *Argonauta*); but in oegopsids, at least a small cone rudiment is always present until advanced postembryonic stages.

In some oegopsids, however, the cone persists as a very large formation in the "larvae" (Textfigs. 71, 73 and especially 72 A). This leads to juvenile forms which are curiously reminiscent of the supposed ancestors (at any rate, of the extinct earlier dibranchiate forms, which I consider to be the belemnoids) and which provide us with an idea of the juvenile stages of these ancestors, hence of the archetypal decapods, indeed of the dibranchiate juvenile stages in general (cf. Textfig. 55).



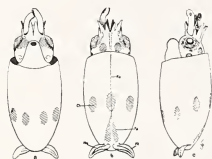
Textfigure 73. — Very young larva of *Pyroteuthis margaritifera* from the plankton of the Bay of Naples. 8× natural size (cf. Vol. I, p. 275).

a) Sketch made after the living animal, completed subsequently. b & c) the same specimen preserved, asymmetrically contracted. Note the shape and insertion of the typical metateuthoid gladius and the insertion of the fins. — bl: blue light organ; gr: green light organ; ld: contracted primary lid covering the lens.

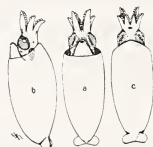
This larva has already undergone some postembryonic development. At hatching it probably was similar to the animal shown in Plate 8, Figures 7 and 8; this illustrates the transition from a short, scoop-shaped gladius to the typical metateuthoid form, especially in combination with Textfigures 74 and 76; whereas Textfigures 75 and 77 already show the degeneration of the vane.

The extreme diversity in shell formation and shell/soft body relationships does not facilitate the definition of a general norm or of the phylogenetic starting conditions, and I consider it my honor to have clarified the picture. The strong regression of the posterior shell portion (which could be compared to the belemnoid phragmocone, hence also to the chambered shell of tetrabranchiates) in the loliginids, and the correlated modifications explained earlier (Vol. 1, p. 473...) for the sepioids, especially the sepiids were not easy to understand, as can be seen, for example, from Abel's (1916) "Palaeobiology of Cephalopods", and the embryonic stages of oegopsids are therefore of special significance in this respect.

In an embryo similar to Figures 7 and 8 of Plate 8 or to Textfigure 72 A, we can easily imagine a replacement of the bowl-shaped cone by the embryonic chamber of a belemnite shell, and even its constriction is understandable with the observation that this part of the body does not contain rather "immobile" organs, but coelomic sacs and the posterior diverticula of the inner yolk organ, which partly replace the coelome; growth continuation in the still regularly conical shell parts must have been related to the progressive resorption of that yolk reserve, which became replaced, in topographical terms, by gas, whereas the coelome withdrew definitively (Textfig. 55).



Textfigure 74



Textfigure 75

Early oegopsid larvae from the plankton of the Bay of Naples.

Textfigure 74. — Very young larva of *Ctenopteryx siculus*. 7× natural size (cf. Vol. 1, p. 253).

— This larva is of special morphological interest, because it belongs to a small group of oegopsids that is far removed from the rest; it retains certain archetypal features of decapods and teuthoids. The overall aspect is quite similar to other young oegopsids, but a striking deviation from the normal pattern is that the ventral arms are already nearly as strong as the dorsal arms. Note also that the fins already show a muscular axis distinct from the membranous marginal part, and that the tentacular clubs are already shortened in an atypical fashion. — Of general interest is the fin insertion on the outside of the gladius, which appears smaller than it actually is due to the marginal encroachment of the muscular mantle, as also can be seen in the subsequent Textfigures.

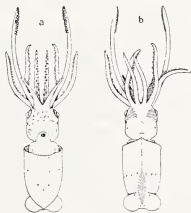
Textfigure 75. — Early larva of an onychoteuthid, 10× natural size (cf. Vol. 1, p. 305). Note the overall similarity of this (systematically remote) juvenile form with Textfigure 74. Here the gladius is not visible from the outside and indeed degenerates (narrows) at an early stage, as illustrated in Textfigure 77. The fin insertion already extends to the tip of the shell cone, as is typical for teuthoids, so the fin is truly terminal.

Given that the late embryonic stages of *Loligo* and other decapods have their homologs only at postembryonic (larval) stages in the oegopsids, it may be useful to recall a number of remarkable data from the first volume, to permit a more complete comparison:

In all oegopsids, arms 3 and 5 attain a stage of development comparable to the youngest *Loligo* (Textfig. 68b) only some, shorter or longer, time after hatching. In this belated development, however, strikingly congruent conditions are typically achieved (Textfigs. 73, 76, 78, 81), as much as the arms at later stages do not reveal
181 their earlier quasi-suppression.

A similar phenomenon, which apparently does not occur in all oegopsids however, is the inhibition of the primary lid development as shown in Textfigure 71 and in Figures 7 and 8 of Plate 8. The connection of the ocular edge with the posterior part ("posterior connecting piece") does not yet occur; the complete formation of the typical organ will be achieved only at postembryonic stages. Unfortunately I have not been able to get sufficiently young larvae of any of these forms to study this process in detail. All the larvae figured here already have a complete primary lid rudiment of the form achieved in ommatostrephids during embryonic development (Pl. 11, Figs. 4-6).

At the hatching stage, the gladius has reached a stage more or less far beyond the condition shown in Textfigure 60 g, in a direction aiming at the general characteristics of Textfigure 60 d, in some forms (going further beyond) of Textfigure 60 c.



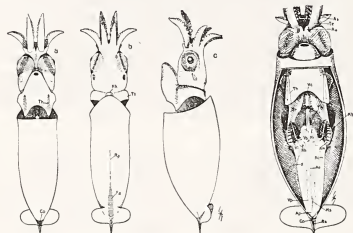
Textfigure 76. — Young larva of *Abraliopsis morrissi* from the plankton of the Bay of Naples. 5× natural size (cf. Vol. 1, p. 290) — This small animal already shows a markedly enlarged arm crown; it must be a successful predator of small planktonic organisms. In addition to a *Loligo*-like overall aspect (Pl. 7; see also Vol. 1, Pl. 1), it shows an even more normal fin connection (with the cone and vane of the gladius and a special terminal tip of the mantle sac) than occurs in the myopsids; this of course results from a further modification of a typically oegopsid preliminary stage as shown in Textfigure 72.

The typical metateuthoid condition (compare Textfig. 77 with Pl. 7, Fig. 4) is not always attained, but sometimes it is already passed over (Textfig. 71 A, B). Unfortunately the material available is insufficient for a precise description and comparison of these interesting conditions:

The young larvae of even the commonest oegopsids (ommatostrephids) are rarely caught, and those available are not the most informative ones. The necessary stages could probably be collected at Messina.

Textfigure 73 shows a larva with an already metateuthoid gladius, but still having a broadly scoop-shaped cone on which the fins are inserted in a still archetypal position (Textfigs. 28, 59, 60).

182 Textfigures 74-78 illustrate the more or less complete regression of the cone, which sometimes bears a purely fleshy tip (76), sometimes a terminal tip stiffened by



Textfigure 77

Textfigure 78

Young onychoteuthids from the plankton of the Bay of Naples.

Textfigure 77. — Older larva, 10× natural size (cf. Vol. 1, p. 306). The mantle sac is somewhat abnormally contracted and thus exposes the posterior rim of the funnel complex, which is normally situated in the mantle. Th: funnel attachment; Tt: funnel pouch; Nk: nuchal attachment.

The third and fifth arm pair are still inhibited in growth. The vane (fa) of the gladius has grown very narrow, and the free rachis (Ra) is partly covered by the muscular mantle. The insertion of the fins also lies partly on the muscular mantle, whereas the rest sits on the persisting, but very small cone (Co). The latter bears a pointed rostrum, which is added posteriorly; it is homologous to the belemnite rostrum, but it is not necessarily a truly belemnoid rudiment (it could be a relapsing homoplasy rather than a homogenetic formation).

Textfigure 78. — A somewhat more advanced onychoteuthid stage with exposed mantle cavity. It shows *Loligo*-like conditions, but in shifted proportions (cf. Vol. 1, p. 308), 8× natural size. A₃: the well-developed third arm; A₄: the still inhibited fourth arm; T: tentacle; Vc: Vena cava; Th: funnel attachment; Tr: funnel retractor; Tb: ink sac; Kb: branchial band; Km: branchial spleen; Rc: insertion on the muscular mantle (after degeneration of the vane) of the head-foot retractor; Ni: kidney papilla; Vs: posterior branch of Vena cava; Kh: branchial heart; Vl: Vena pallialis lateralis; x: primary position of the gladius rim; Ao: Aorta posterior; Vp: Vena pallialis posterior; Ms: mantle septum, still situated markedly posteriorly; Ap: Arteria pallialis posterior; Co: cone; Rs: rostrum.

a true rostrum. The insertion of the fins concomitantly is shifted towards the body end (something certainly atypical for decapods), while their anterior edge grows out in the cephalic direction. By this process the fin base is moved more or less markedly from the shell onto the muscular mantle, which in its turn has embraced the shell rim and thus placed the shell inside the mantle (cf. Vol. 1, pp. 156-157). What appears by translucency (Textfigs. 76 and 77) as the "lanceola" (*sensu* Pfeffer) indeed does not represent the whole gladius, which lies partly inside the mantle, but only the part covered by the thin shell epithelium which is not covered by the muscular mantle.

2. The Embryonic Development of the Oegopsid X

The embryos described here and figured on Plate 8 are from an egg mass collected at the sea surface near Naples in September 1900; a more detailed description of this egg mass is not available. The preserved material at my disposal permitted recognition of the typical chorion surrounding the egg and gelatinous material adhering to the chorion, which probably formed one big egg mass as is typical for oegopsids. Jatta (1896, p. 96) apparently obtained similar eggs from Messina; he identified them as "*Veranya sicula*", that is *Octopodoteuthis*. Whether this identification was correct can no longer be verified since his material has been lost. Lo Bianco (1909, p. 657) used that description for the identification of the present material, and there is no reason to doubt his identification. But given the tentacle formation, it can be excluded that this egg mass is from *Octopodoteuthis*; in the latter genus the tentacular clubs are very characteristic (Vol. 1, p. 337). They would then have a maximum of 8 suckers each. Likewise the present material cannot be considered the same species (Jatta, loc. cit.) as the embryos described by Grenacher, as can be seen by comparison with Grenacher's figure of a mature embryo (Textfig. 70) with Textfigure 72.

The present oegopsid X is either *Calliteuthis reversa*, *Histioteuthis bonelliana* or *Thysanoteuthis rhombus*; it cannot be an ommastrephid (Pls. 9, 12) since the embryonic stages in this family look very different. Oegopsid X is not a chiroteuthid either, nor an onychoteuthid, because the known juvenile forms do not correspond in size or morphology. For the same reasons the enoploteuthids, *Ctenopteryx*, *Octopodoteuthis* and *Brachioteuthis* can be excluded. In any event, it must be a large, typical oegopsid with primarily separate fins, of stocky shape, and with a typical larval brachial apparatus.

Each tentacle bears 10-12 suckers arranged in 2 rows. The relationship with ommatostrephids cannot be a close one, which pleads against *Thysanoteuthis*.

This material contained a few younger stages (I-VIII), but they were so poorly preserved (probably fixed *post mortem*) that I refrain from any further description. The remaining embryos were only slightly different from the 4 figures on Plate 8, which must suffice for our considerations. Even in these embryos only a trained eye could see all the details figured; the material is completely leached, the chromatophore colors gone long ago.

Stage VIII-IX (Pl. 8, Figs. 1 and 2) shows the yolk sac (do) rudiment as an inconspicuous, rounded elevation surrounded by the anlage of the arm crown (II, V), which here again appears as a completely closed, rib-like ring.

184 The latter shows on either side three to four inconspicuous elevations, which are the dorsal arm rudiments of the first and second pair (I, II), ventrolaterally the tentacle rudiments (IV), close to which the ventral arms (V) are barely visible. In a dorsal view the rest of the anterior half of the body is represented by the cephalic anlage, which shows the eyes in lateral position and the buccal rudiment medially, each of them appearing as a transversally oval annular fold. In the anterior part of the buccal rudiment, the point-shaped invagination of the poison gland rudiment (gd) is already visible; it will migrate posteriorly and soon become covered by the posterior rim of the mouth. The anlage of the central nervous system appears as a bright, low elevation surrounding the eyes and extending ventrally, and with a narrow dorsomedial connection; it will soon become subdivided into the cerebral ganglia, the optic ganglia and the white body. For the moment it is merely a poorly delimited, diffuse proliferation of the ectoderm. Ventrally and slightly medially from the eye mass the ring-shaped statocyst rudiment is recognizable on either side.

Between the statocyst rudiments, the funnel tube fold arises, its lateral parts being more distinct, while medially a depression marks the prospective funnel opening. The connection with the funnel pouch rudiments has just been achieved behind the statocyst rudiments; the funnel pouches seem connected (cf. p. 104) by a light belt tie (gb) that lies behind the funnel tube folds. The gill rudiments lie further posteriorly; they appear as very low knobs, between which the anal projection is even less distinct.

The mantle fold is a belt-like, low rib which is dorso-medially (ma) almost interrupted, i.e. at the prospective site of the proostracum which will complement the muscular mantle. The darker rounded area lying further posteriorly marks the position of the prospective scoop-shaped "conus"; it does not yet exist at this stage, and its actu-

al area is not yet entirely occupied by the shell sac. On its dorsal side we find the familiar anchor-shaped pattern of Hoyle's organ, each lateral branch reaching to a fin rudiment.

Stage X (Pl. 8, Figs. 3 and 4) shows the same general arrangement of the parts, which are now more advanced in their differentiation. The arm rudiments are more distinct; the buccal rim is more contracted and now covers the poison gland rudiment. The eye vesicles are now completely closed, and the anlage of the central nervous system is more clearly differentiated. The cerebral ganglia appear rather distinct (as bright spots between the mouth and the eyes), similarly distinct are parts of the white bodies behind and below the eye.—The funnel folds are more markedly elevated, and the typical anlage of the funnel tube becomes recognizable. The mantle fold has grown forwards and begins to cover the gills and the anal area. The prospective shell complex shows a beginning differentiation into a proostracum and a cone; the former occupies
185 the dorsal gap of the muscular mantle.

Stage XVI (Pl. 8, Figs. 5 and 6) is much more advanced; it shows a state after completion of the essential phase of differentiation: the yolk sac is a small wart between the arms, in a position corresponding to the last remnant in loliginid larvae (Pl. 7). The two dorsal arm pairs are short appendages with one sucker each; the arm pillar reach backwards over the head, but remain strikingly delicate as if retarded, comparable to stage XIII of *Loligo* (Pl. 5, Figs. 1 and 2). As there, the mouth is not yet covered by the dorsal arms; so here a peculiar inhibition of development appears, which seems to be more or less typical for oegopsids, which could be related to the temporary suppression of the third arm pair. There is no actual primary lid fold yet; the eye region as a whole thus is retarded at this stage.

This retardation is less striking in the ventral aspect, because the tentacles are well developed. The differentiation of the arm pillars corresponds roughly to stage XIV-XV in *Loligo* since the posterior end of the lateral edge clearly approaches the eye. The ventral arms are still stub-like.

The funnel apparatus is rather well developed; even the nuchal attachment rudiment appears to be there. The funnel corners show the typical primitive mantle connection turned up, and the retractors are well developed. The body part lying inside the mantle is blown up by the yolk and partly exposed due to the retraction of the mantle. The anal papilla begins to become organized, and the gill rudiments show first signs of gill lamellae in the form of small lateral papillae. The mantle sac anlage is fully formed. In a ventral view one can see the rim of the cone project medially, something

I have seen also in the youngest histioteuthids (Vol. 1, p. 354), and on the dorsal side the anteriorly acuminate proostracum is clearly visible through the surface, with the stellate ganglia on either side (cf. Textfig. 72). On the dorsal side of the cone, close to the posterior end, the small lobes of the fins are set far apart, connected by the lateral branches of Hoyle's organ in the typical fashion (Pl. 7).

Stage XVIII (Pl. 8, Figs. 7 and 8) represents a rather fully developed embryo that is not very far from hatching. Its organ development nevertheless lags markedly behind that of a mature embryo of *Loligo*. The brachial apparatus and the yolk sac show the general overall picture as the preceding stage, but close inspection of the dorsal side reveals the fact that the cephalic envelope has largely caught up to compensate the earlier delay by covering the mouth and making progress in the lateral advance of the ocular edges. Although the third arm pair is not visible from outside, its rudiment can be supposed to be there; indeed we know (Pl. 6, Figs. 2-5) that the dorsal ocular edges belong to the third arm pair, not to the second. The keels of the dorsal arms take a peculiar course.

186 On the ventral side of the head, no notable progress has been made by the cephalic covers; thus its development now is retarded, and the corneal fold rudiment of this mature embryo is still at a stage corresponding to XIV-XV of *Loligo*. The youngest pelagic larvae of oegopsids demonstrate that this fold is sometimes completed only during postembryonic life (cf. Textfig. 70). The eye proper is equipped with a lens and a functional iris fold.

The mantle sac shows the features already mentioned for the previous stage, but it has grown in length and its cavity in depth; on the ventral side the gills and the anal papilla shine through the mantle. The fins appear to approach each other at the posterior body end. The fact that the dorsal corner of the mantle edge is replaced by an indentation is probably due to tissue contraction, whereas ventrally a normal, though narrow, indentation accommodates the funnel tube.

3. The Embryonic Development of the Ommatostrephid Y

The following description of ommatostrephid development is based on observations made on three egg masses of probably the same species (as far as can be judged from available material and from sketches made of the living specimens), at least of

the same subfamily (Ommatostrephinae). It is highly likely that we are dealing here with *Stenoteuthis bartrami*, perhaps partly with *Ommatostrephes sagittatus*. These egg masses were found floating at the sea surface near Naples; they contained very large numbers of eggs embedded in a jelly mass. No detailed descriptions are available for this material. The three egg masses were observed on 12 September, 1901, on 17 October 1901, and on 28 September 1904, respectively. Each of them was kept in the aquarium for a few days, sketches of the embryos were made and samples were fixed at intervals until the young larvae hatched; this developmental time appears to be very short (4-6 days) in these animals. This material does not permit description of the very early stages; the available sketches do not give much information on them, and I therefore begin my description at stages showing surface structures.

The eggs measured 1-1.05 mm in length and 0.8-0.9 mm in width (according to the indications provided by Dr. V. Bauer who made sketches of the embryos and preserved the material). The drawings show them to be nearly spherical. The chorion, the micropyle and the polar bodies are visible in their typical form.

187 Stage VIII (Pl. 9, Figs. 1-3) largely corresponds, in terms of general differentiation to the same stage of *Loligo*, but differs from the latter in the arrangement of its parts which we found to be typical for the oegopsids (p. 180); it thus resembles the embryo of oegopsid X.

The yolk sac is represented by a barely convex, small field at the anterior pole; it is surrounded by a bright, only slightly elevated strip which is the arm crown anlage. In the latter, individual arm rudiments can already be seen as portions of the strip that are defined by slight constrictions, again three on either side (I, II, III on the Plate; note that this is a copying error: it should read I, II and IV in Fig. 1, and III, IV in Fig. 2 of Pl. 9). The cephalic anlage with the mouth and the eyes shows no particular feature. The statocyst rudiments are not yet clearly recognizable, i.e. they are slightly retarded. The funnel rudiments (tr), the "belt strip" (gb), the gills (km) are represented by barely elevated bright strips, like the muscular mantle (ma) which narrows dorsomedially to become a very narrow strip, since the shell zone here projects forward with the prospective proostracum (pr). The posterior pole shows a bright spot (ho₁); in apical view (Pl. 12, Fig. 1) this spot can be seen to be arranged around the closing pore (sp) of the shell sac; it is still undifferentiated (x) and will later form the fin rudiments. The typical three delicate furrows marking the prospective organ of Hoyle radiate out from this pore. Later on (Pl. 12, Fig. 3), the portion of the cell material that is adjacent to the lateral branches (fl) becomes elevated on either side and forms a papilla:

the paired fin rudiments which are connected, in typical fashion, by the organ of Hoyle (Cf. Pl. 2, Figs. 11-12).

At stage X (Pl. 9, Figs. 4-6) the folding process is already more advanced. The three arm rudiments on each side are distinct knobs, their size increases in ventral direction (I, II, IV). The ocular fold is contracted completely or almost completely (leaving a small scar), so that the eye vesicle (au) is now closed. The statocyst (st) is a pit surrounded by a rim that is more elevated medially; the funnel tube rudiment shows the structure typical for this stage. The belt strip (gb) behind the funnel is still very distinct and laterally connected to the funnel rudiment; the funnel pouch rudiments (tt) are inconspicuous ribs. The gill rudiments (km) are still indistinct, barely convex and markedly drawn out laterally; the muscular mantle (ma) forms a sharp annular fold except for the small nuchal area (Fig. 6) which marks the prospective nuchal attachment and the position of the proostracum. Figure 5 shows that this embryo already has some yellow-reddish chromatophores on the mantle and on the arm crown.

For better understanding of this stage, one should note that, except for the more massive anlagen, the cellular formative material that will provide the major tissue mass of the embryo is still a very thin envelope surrounding the yolk. The same can be said for the next stage.

188 Stage XII shows an embryo which already hints at the topography of a young cephalopod, exhibiting the primary positional relationships between the parts of the animal. The knob-shaped arms (I, II, IV) begin to extend arm pillars posteriorly; the cephalic anlage becomes subdivided and shows the increasingly prominent eyes surrounded by elevations forming the eye stalks (Cf. Pl. 4), which contain the rudiments of the white body. The statocyst openings are narrow, the funnel tube is closed and laterally connected to the funnel pouches; from this typical connection the funnel retractors depart. The mantle (ma) has become cup-shaped and surrounds a slit-like mantle cavity ventrally and laterally, whereas dorsally a free edge is only beginning to form. The mantle gap corresponding to the proostracum is still very broad and still outside the domain of the mantle cavity. (For the fins 'fl' and Hoyle's organ see above)

At stage XIV the arm crown is strongly contracted, pushing the yolk sac (do) forward; the individual arms are also more distinct, especially the prospective tentacles (IV), and show larval sucker rudiments: the arms of the upper two pairs each bear a sucker rudiment in almost terminal position, each tentacle bears 4 sucker rudiments,

one of which sits at the tip. The latter suckers are not symmetrically arranged; the proximal three suckers are arranged so that on one tentacle 2 suckers are in the medial row, one in the outer row, whereas in the opposite tentacle the inverse happens. Each arm rudiment extends a distinct arm pillar to the head (pf1, 2, 4). The ventral pillars reach further backwards than the dorsal ones (p. 191). Compared to the oegopoid X, it is noteworthy that at this stage distinct ventral arm rudiments are still lacking; they are represented by the undifferentiated material lying between the bases of the tentacles.

The cephalic anlage has made further progress in differentiation and the eyes now appear somewhat stalked. The eye proper has a lens and an iris fold, both formed by the typical process. The statocysts are closed, but they still lie immediately under the skin surface between the funnel and the cheek complex and are visible as bright, slightly convex spots. The posterior part of the funnel apparatus, which is complete except the nuchal and mantle attachments, is now inserted in the mantle sac.

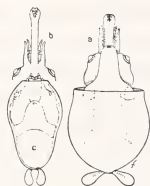
The mantle sac has made important progress in several respects: the shell zone is regressive and particularly narrow in the part containing the proostracum. Here the muscular mantle has pushed its insertion onto the outside of the shell sac, as seems typical for this family; in the anterior part the mantle muscle appears to embrace the shell entirely so that the tube is completely closed. In the posterior part the proostracum is still visible as a narrow shell process, partly hidden by the anterior branch of Hoyle's organ. For the latter and for the fins, see Figure 4 of Plate 12.

189 Stage XVI (Pl. 10, Figs. 4-6; Pl. 12, Figs. 5 and 7) comes fairly close to the general aspect of a mature larva: the arm crown is now more strongly contracted and constricts the small yolk sac, which has the form of a slightly more than hemispherical wart.

The two dorsal arm pillars (pf) have formed quite typical cephalic covers, the ocular edges of which join very closely the posterior end of each eye ball. The mouth (mu) is now becoming submerged below the dorsal arms which join each other. The ventral aspect reveals more important features: the pillars of the tentacles (pf₁) are still retarded, and the edges facing the eyes do not show any indication of a lid formation. Their developmental stage corresponds to about stage XIII of *Loligo* (Pls. 5 and 6). The two tentacle rudiments closely join each other in the median line and their base already shows an early sign of fusion (nt). This is the beginning of a modification that is highly characteristic for the family, leading to the peculiar "*Rynchoteuthis*" larva.

The "proboscis" of this larva (Textfigs. 79 and 80) is nothing other than the product of the joint tentacles (cf. p. 23). At their base, situated submedially close to one another, the two ventral arms (V) are visible as low papillae. This is a condition corresponding to what the embryos of the oegopsid X show from the outset, since the latter have inconspicuous, yet clearly recognizable ventral arm rudiments as a primary condition (Pl. 8, v). (In both embryonic forms of oegopsids—and in all the early postembryonic stages so far studied—the third arm pair is still missing as far as the surface aspect indicates.)

The cephalic anlage has changed in that the eyes are now directed forward, the embryonic form thus being transformed into the typical larval configuration (cf. Pl. 5). The same can be said of the mantle sac: it now appears slightly pointed posteriorly, the fins remaining separate (Pl. 12, Fig. 5) but set close to each other. They are strikingly small, rounded lobes. The anterior mantle end is also slightly constricted, its rim showing the typical form: ventrally there is a small, shallow indentation for the funnel,



Textfigure 79



Textfigure 80

Earliest post-embryonic ommatostrephids, so-called "*Rhynchoteuthis*" larvae. From Volume 1, page 421.

Textfigure 79. — Stage XX of the ommatostrephid Y hatched from an egg mass kept in the aquarium; drawn as in life. This figure was combined from live observations and drawings made after preserved material. 20× natural size.

a) In normal swimming position, seen from below. Tentacular "proboscis" one half extended, ready to catch a prey animal.

b) Fully extended proboscis, in which the clubs begin to diverge in preparation of seizure.

c) Typical contraction of young oegopsid larvae. The head is fully retracted into the mantle sac, the proboscis extremely shortened.

Textfigure 80. — Youngest "*Rhynchoteuthis*" larva collected in the plankton at Naples. 15× natural size.

c) Lateral view of the preserved specimen, the mantle sac being strongly contracted thus exposing the posterior rim of the funnel complex. The gills are also largely exposed.

b & a) The same specimen in dorsal and ventral view, reconstructed after live observations.

flanked by slightly projecting corners (ve). Dorsally and medially, the projecting corner that should be expected to exist there is replaced by a slight indentation (de), as in stages XIV, XVIII and XX, and in the oegopsid X. Perhaps this is due to the contraction of the mantle during fixation. The number of chromatophores has increased.

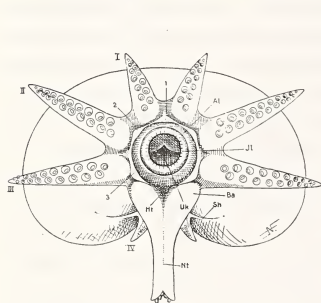
Stage XVIII (Pl. 11, Figs. 1-3; Pl. 12, Figs. 6 and 8) is even closer to the condition of a mature larva: the arms are slightly longer, and the 4 dorsal arms each have a tip reaching markedly beyond the sucker. The yolk sac is reduced. The tentacles are joined over a long distance, up to the base of the short clubs; the latter turn their faces carrying 4 suckers each obliquely forward. (But see also the live habit shown in Textfig. 80). These two faces are in fact united in one, the line of fusion forming a
190 broad seam that forms the end of the longitudinal fusion seam of the stalks. At the base of the "proboscis" thus formed, the small rudiments of the ventral arms lie in the same position as before. The ocular edges of the two head covers now bend on either side around the posterior end of the eye ball and are united by a small "posterior connecting piece" to form the lid anlage; thus, in contrast to the oegopsid X, the lid fold is already established during embryonic development.—On the ventral side of the head, the olfactory tubercles are differentiated on the "cheek" area.—The fins are now more strongly developed, but for the rest the mantle sac shows no noticeable new features.

State XX (Pl. 11, Figs. 4-6; Pl. 12, Fig. 9) corresponds to a fully developed larva, perhaps a few hours (? or days?) after hatching, which lived in the aquarium according to the indications given on the drawings. (Figs. 4-6 were made using the sketches prepared earlier from live observations by the station's artist V. Serino.) This larva is different from the embryonic stage XVIII in the more marked differentiation of the surface features:

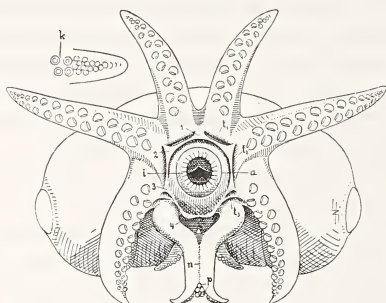
The arms are longer and finely pointed, the proboscis is functional (cf. Textfig. 80). The lid fold is contracted around the eye ball, of course with a variable opening; in a relaxed state it shows a circular outline without a sinus. The funnel is strongly
191 enlarged and can be extended even further in life; the mantle sac in its turn is extremely extensible, becoming much more voluminous than in the figure, which was made after a preserved specimen. The fins now are spatular, the very mobile and also extensible lobes showing the typical aspect of very young teuthoids (Pl. 7).

The mantle cavity (cf. Pl. 8 and Vol. 1, pp. 425, 427) would show the typical conditions of young oegopsids which are of no special interest here: the gills are very poorly developed, minute warts with few lateral warts (Textfig. 79) representing the

first gill lamellae. A stage of differentiation corresponding to the youngest loliginid larvae (Pl. 7) is reached only after some considerable time spent as a free larva. Similar features are revealed by the arm crown development: to illustrate these aspects, Plate 12 shows the buccal field of two somewhat older larvae. They show that the buccal lappets are still lacking (cf. p. 132), that the third arms (III) are formed very late but then catch up soon and that all arm tips add new suckers (sn) which are arranged in alternating rows beyond the existing ones. The "proboscis" will never have more than the eight embryonic suckers; it is only after the beginning of tentacle separation that the hitherto inhibited clubs grow further and develop new suckers for the establishment of the adult club structure (Textfigs. 81 and 82): a peculiar feature, especially for people accepting the so-called fundamental biogenetic law, is the fact



Textfigure 81



Textfigure 82

Buccal fields of advanced *Rhynchoteuthis* stages from the plankton of the Bay of Naples.

Textfigure 81. — Probably *Ommatostrephes sagittatus*. 25× natural size. From Volume 1, page 426. Climax of the larval development.

The third arm pair (III) is already the strongest, whereas the fourth (IV) lags behind the others. The bipartite structure of the proboscis is very distinct; at the base of the tentacles (Ba) the seam (nt) is already stretched into a thin membrane (Ht), which will soon be torn apart (Textfig. 82). The 5 upper buccal lappets (1-3) are visible at their normal positions, whereas the ventral ones are hidden.

Uk: lower beak; Sh: rudiment of swimming membrane, growing from the 4th to the 3rd arm; II: inner lip; AI: outer lip.

Textfigure 82. — Juvenile stage of *Stenoteuthis bartrami*, 20× natural size. From Volume 1, page 462. Beginning separation of larval tentacles. The growing arm tips show sucker rudiments in a straight, single file; this is shown in detail in the inset figure of the tentacular tip (45× natural size); the 4 proximal suckers (k) are the only ones that functioned in the larval "proboscis". The main figure illustrates the progressive change from the larval structure to the definitive condition via the separation of the tentacular stalks. Note also the buccal funnel anlage with the typical arm rudiments 1-4.

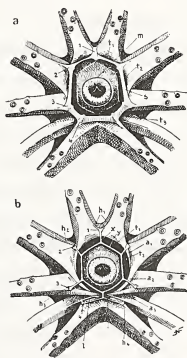
i: inner lip; a: outer lip; t1-5: buccal pouches; n: seam; p: larval tentacular suckers.

that the entirely typical decapod conditions (compare Textfig. 83 with Vol. 1, p. 179) are preceded by highly abnormal larval formations, so one might conclude that in ommatostrephid phylogeny a rhynchoteuthis stage existed, from which again archetypal conditions were achieved secondarily.

But even for a more critical consideration of such relationships, the facts are not easily interpreted. A gross view indeed indicates that the normal conditions of the buccal field in older ommatostrephids is materially derived from the rhynchoteuthis form (Pl. 12); therefore the latter should have a higher degree of generality (p. 24) and thus would be typical for a greater systematic group, hence should be considered more primitive. A careful analysis of the processes figured in Figures 7-11 of Plate 12 and in Textfigures 81-83, which end in an almost typical decapodan condition (cf. Pl. 22) demonstrate, however, that in fact no typically developed part is derived from atypical stages of the same anlage material; that quite to the contrary, the peculiar combination of larval features present in the rhynchoteuthis stage is due to two factors that are by no means concerned with morphogenetic details, but only with the overall image and functional correlation of forming parts at certain stages.

The following can be recognized as these factors: a) a markedly heterochronic shift of processes, by which the normally combined or immediately successive states become separated, and b) the formation of an actually minor larval organ, which modifies the mutual relationship of the parts in a striking and effective manner.

The transitory inhibition of the ventral arms places the bases of the tentacular arms of oegopsid larvae particularly close to one another (cf. Textfig. 77), sometimes leading to actual contact of the tentacles even in non-ommatostrephids. This permits the formation of a connecting skin fold which is so inconspicuous that it has not always been recognized



Textfigure 83. — Buccal field of a modestly specialized ommatostrephid: *Illex coindetii*, in natural size. From Volume 1, page 240.

The arms have been spread out in the fresh specimen, prior to preservation. 1-4: buccal arm rudiments (buccal lap-pets); t_1 - t_3 : buccal pouches; m: outer lip (primary buccal edge).

as a special differentiation; in our description above it has indeed been passed over in the formula (p. 196) that the tentacle rudiments "become connected" starting from the basis. The position of the suckers (Pl. 10, Fig. 5; Pl. 11, Figs. 2 and 5) shows that the statement about progressive fusion towards the tip is not entirely correct either: in fact the fused basal parts of the tentacles, which represent the stalks, grow in length and push the tiny clubs forward.

What connects the tentacles with one another is a special, separately acting cell material of the tentacle epithelium facing each other: it connects the tentacles so as to make them appear a single formation, without impairing their prospective significance. This cell material will disintegrate at a later stage, either according to its formative potency, or directly caused by cell necrosis (more about that further below), and its development then ends; in contrast, further differentiation of the tentacles goes on without any inhibition. Thus here we see a larval organ as defined earlier (p. 23) and its later disappearance. For normal development of oegopsid tentacles, see Volume 1, p. 235.

The anlage material for the later-formed, absolutely typical differentiations, indeed undergoes the typical preliminary developmental processes, but partly in premature, partly in belated ways and thus in an atypical combination, which is further enhanced by a transitory embryonic/larval formation.

This transitory formation behaves like other morphologically independent parts in that it undergoes a constructive development (morphogenesis), which could be interpreted in phylogenetic terms according to the general scheme. Moreover, I am aware of forms that exist either among the ommatostrephid (the secure identification of such a pararhynchoteuthis larva from the Atlantic in Chun's material is not yet possible) or in related forms, in which the tentacles (after a stage corresponding to Fig. 5 of Pl. 10) are free but lie close to one another and grow out in a columnar fashion (Pl. 11, Fig. 194 2), after which they appear similar, perhaps somewhat less perfect and solid. One can suppose that preommatostrephids existed, in which only a part, then others in which all of the tentacle stalks, was fused, and finally forms in which the tentacular club became specialized. In the extant Mediterranean representatives of the family the "proboscis formation" is always complete (I do not know whether this applies also to exotic genera like *Hyaloteuthis* and *Euclideanoteuthis*, which lie somewhat apart).

Of course, here we are dealing with a larval adaptation that may facilitate rapid growth of the animal. In many other oegopsids, we see typical devices for the attachment

of one tentacle club base to the opposite club base, allowing an efficient coordination during tentacle ejection (more appropriately named "shooting"), thus improving accuracy of capture. (See "adhesive apparatuses" in Vol. 1, pp. 228-229) This accuracy is already remarkably high in animals having separate tentacles, as can be seen in any *Sepia* (cf. Vol. 1, p. 553!), so Textfigure 79 allows one to surmise that the "proboscis" is indeed an excellent prehensile gear for a small plankton hunter.

CHAPTER 8

On the Embryonic Development of the Sepioids, Namely of the Genus *Spirula* and its Closest Relatives Both Living and Fossil

Contents: 1. Generalities. 2. On the Embryonic Development of *Spirula* (p. 208). 3. On the Modification of the Sepioidea (p. 210).

1. Generalities

For the characteristics of sepoid development remember the earlier statements (p. 153). So far as the ontogeneses of sepiids and sepiolids can tell, there is a series of special features of the suborder, especially in embryonic stages. Unfortunately we know nothing about the development of the idiosepiids, however, and for *Spirula* we can only make some inferences from the later postembryonic stages, from the embryonic part of the shell, and from the mature ovarian eggs. In fossil forms we know, in the best of all instances, the embryonic shell parts that allow us to make comparisons with corresponding parts of the *Spirula* shell. Thus we can make general statements on sepoid embryos only with great reservation, and what we say can be valid only for the
195 limited extent of facts just circumscribed.

The eggs of sepoids are always laid singly on the sea bottom, and wherever large clusters are produced, they are due to progressive accumulation of single eggs at the

same spot. It never occurs that numerous eggs are surrounded by a common jelly envelope. The ova are always relatively large, sometimes extraordinarily large if one considers the small body mass of most adults, especially in sepiolids. Within the decapods, these eggs represent the maximum size, which corresponds roughly to the relations observed in large-egg octopods (p. 71). This relates to the fact that the morphological endowment of the newly-hatched animals is very complete, differing from the adults virtually in quantitative terms only. The sepioids hatch as young animals living in a way very similar to that of the adults, not as "larvae" having a markedly special, e.g. planktonic life style.

The germinal disk is rather small at the outset (Pl. 13). (*Rossia* and *Sepia* are very similar in this respect: in *Rossia macrosoma* the diameter of the germinal disk at stage II is about 1/8 of the minor egg diameter, in *Sepia officinalis* it is about 1/5). Cleavage shows the typical features of decapods (p. 144). It leads to the formation of a blastoderm (Pl. 13, Fig. 6) that has a strikingly irregular contour, with pluricellular marginal processes grading into delicate plasmatic strands which radiate out on the yolk surface. Formation of the lower layer (the endomesoderm) becomes visible in the form of a closed ring, so that the germ axes are no longer recognizable. The plurilayered ring grows rapidly broader (Pl. 13, Fig. 7) in both centripetal and centrifugal direction; in the latter direction it overtakes the marginal rays of the germinal disk which are simultaneously retracted (p. 102). In this process, their cell complexes grow looser, providing the impression of cells being scattered on the yolk surface (Pl. 14, Figs. 1 and 2); detailed observations show, however, that the number of yolk cells lying outside the ring decreases rapidly.

Finally all yolk cells are hidden below the germinal disk (Pl. 14, Fig. 3), the darker, monolayered central part of which narrows down progressively (Pl. 14, Fig. 4). At this stage the actual mesoderm formation below the ectoderm has already begun and now continues (Pl. 14).

The folding up then starts (Pl. 15) to form an embryo disk showing the basic features already described for *Loligo*. There are 10 distinct arm rudiments from the beginning, even though the first, third and fifth arm pairs can be retarded. Sometimes all the arm rudiments are exactly alike in their respective developmental progress (Pl. 23). A more striking and significant feature is the bipartite appearance (cf. p. 107) of all the arm rudiments in sepioids (Pls. 15 and 23). It looks as if each arm were made of two similar elements, although their morphological value and phylogenetic significance

cannot yet be interpreted safely. The phenomenon fades away during later develop-
196 ment, although traces can be seen for some time in the form of a delicate longitudinal
furrow on both the inner and the outer side of the arm (Pl. 17, Fig. 3). The inner fur-
row disappears in connection with the sucker formation, whereas the outer furrow
marks the site of the prospective glandular cell lines (Pl. 16; Pl. 18, Fig. 1), but a
direct relationship with them is not recognizable. More advanced embryos show some
general similarities that are not easily definable (Pls. 16 and 23); a trained eye picks
them up immediately, however. An essential feature appears with formation of the pri-
mary lid fold, which here can be called corneal fold. This is not of course a basic dif-
ference from the teuthoids, but only a gradual one: the corneal fold is made from the
4 typical elements: ventral and dorsal ocular edges of the corresponding arm pillars or
head covers (Pls. 16 and 17) plus anterior and posterior connecting pieces. The head
covers show no special features, no more than the anterior connecting piece (vb),
which is distinctly visible between the third and fourth arm rudiment in Figure 2 of
Plate 23, i.e. at a stage when the other parts are not yet recognizable as such.—But the
posterior connecting piece shows up in a very peculiar manner: it arises very early
(before the head covers have attained a closer relationship to the eye) as a distinct, deli-
cate rib or edge of considerable length (Pl. 16, Fig. 5, hb); the posterior ends of the
two ocular edges (cf. Pl. 23, Fig. 5) become dorsally and ventrally connected to that
edge only secondarily.

This piece of the corneal fold thus appears as a perfectly distinct formation, and
it remains so up to the moment when the ring is closed (Pl. 16, Fig. 7), after which it
is integrated in the whole in a typical fashion (Pl. 18, Fig. 1). The part it takes in the
formation of the ring is apparently rather important, even though this particularly deli-
cate piece may later contract and thus become less conspicuous. In other decapods
(Pls. 29 and 35) the posterior connecting piece is a very minor part of the primary lid,
and it took long and careful observations to be certain that it is not absent. Superficial
inspection of preparations made before and after the constitution of the primary lid
may indeed lead to the impression that the upper and lower lateral edges simply meet
behind the eye. Very careful investigations into very many stages led me to the con-
viction that this is never the case, i.e. that the posterior connecting piece is never
entirely suppressed in the formation of the primary lid fold. For the morphological
understanding of this formation, i.e. for the insight into its complex origins (being
derived from both the arm apparatus and the primary cephalic epithelium), the

evidence given by the sepioids is indeed essential, and it provides a further, important indication for the close relationship among the sepioids, especially of the sepiolids 197 and sepiids which appear so different in other respects.

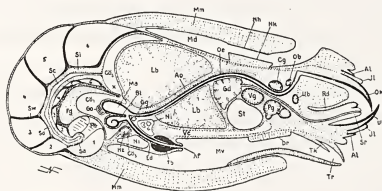
In the sepioid embryos so far known, the fins undergo a secondary modification of their most important correlations, in a way similar to what we have seen in the teuthoids (p. 111), but more markedly so: first they are situated in an archetypal position (Pl. 15, Fig. 4; Pl. 23, Fig. 2) on either side of the shell sac pore, which marks the mantle end, and their posterior edge encroaches on the future ventral side; later they shift forward (Pl. 15, Figs. 4 and 5; Pl. 16; Pl. 23, Fig. 3, 5, 6, 8) and their posterior edge acquires its definitive relation with the lateral branches of Hoyle's organ. (For comparison see the generally much more direct development of the teuthoids, as shown in Pl. 2, Figs. 10-12, and Pls. 7, 8, 10, 12, where the definitive condition is recognizable almost from the beginning.)

This minor modification of the bauplan can be interpreted phylogenetically in considering the conditions of conservative sepioids (cf. Vol. 1, p. 516: *Spirula*, p. 592: *Idiosepius*, p. 496: *Spirulirostra*). Textfigures 85 and 86 show that in the sepioids a fin position encroaching on the ventral side must be archetypal, so the question arises whether the dorsal shift observed in sepiids and sepiolids arose independently from one another, or whether it reflects a common preliminary state. In the latter case, *Idiosepius* would have to be a participant in it (Vol. 1, p. 503).

On the other hand, one should remember that the supposedly archetypal condition of the sepioids is not unique. A similar condition is known from teuthoids in which the interrelation between the shell rudiment, the mantle and the fins is fully expressed at early larval stages (Textfigs. 70 and 71); and the same condition can be considered archetypal for such stages in general (Textfig. 55). Alignment with the longitudinal axis of the animal (Textfigs. 75-78) then is a secondary condition that has been obscured, suppressed or re-established in differing ways in the different decapod groups. One might even surmise for the adult stage of archetypal dibranchiates (vol. 1, p. 91) and decapods (Vol. 1, p. 110) that the fin insertions were oblique and lateral on the shell surface, with a tendency to reach ventrally, and that this condition proved phylogenetically successful only in the sepioids (cf. Textfigs. 28 and 30). But the overall features of the older fossil types plead against this hypothesis.

Other peculiarities appearing in sepioid ontogenesis are of lesser systematic significance, since they are part of their general morphological and biological features

(p. 203), and are especially related to the yolkeness of the eggs: 1) the larger, more archetypal forms have 4 rows of suckers on their arms and even more numerous (normally 8) rows on the tentacular clubs, where they show a very specific arrangement (Vol. 1, p. 488). 2) The mantle organs, especially the gills, already attain a high degree of differentiation in the embryo (without forming a longitudinal canal in the gill as in teuthoids: Vol. 1, pp. 73, 489). 3) The funnel attachments and the nuchal attachment (as far as it is retained) are already formed in young embryos (Pls. 17, 23), whereas in the teuthoids they appear only during larval life. 4) Unless a new adaptation to nektonic life has occurred, a secondary lid fold develops in the periphery of the contracted, corneal part of the primary lid.



Textfigure 84. — Diagrammatic medial section of a young *Spirula*. From Volume 1, page 475. — 14× natural size.

Note the general shape of the shell and its position in the body, especially the situation of the shell aperture among the viscera; note also the atypical insertion of the muscular mantle on the outside of the gas chambers, ventrally behind the rotated initial chamber. The lack of a proostracum is striking; it allowed the atypical shift of the dorsal shell rim to the inside of the body. In the position vacated by the shell rim, the muscular mantle has taken over; it naturally lacks in the rest of the dorsal midline (See Textfigs. 28 and 30). 1-6: gas chambers; Ps: prosiphon; Sa: initial caecum of siphuncle; Sd: septal neck; Sw: shell septum; Sc: siphuncular coelom; Si: fleshy siphuncle; Fg: filling tissue; Co1-C63: parts of coelom; Go: gonad; X: ventral shell rim; Bl: caecum; Hz: heart; Gg: stomach ganglion; Ni: kidney; Mm: muscular mantle; Ed: hindgut; Tb: ink sac; Af: anus; Mv: mantle cavity; Vc: Vena cava; Lb: liver; Ao: Aorta; Md: dorsal mantle cavity; Oe: oesophagus; Gd: poison gland; St: statocyst; Vg: visceral ganglion; Nk: nuchal attachment; Kh: cape attachment; Cg: cerebral ganglion; Pg: pedal ganglion; Ob: upper buccal ganglion; Ub: lower buccal ganglion; Dr: funnel gland; Tk: funnel valve; Tr: funnel tube; Al: outer lip; Sr: subradular organ; Jl: inner lip; Uk: lower beak; Ob: upper beak; Rd: radula pouch.

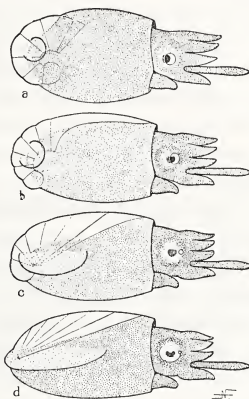
The archetypal mode of shell formation, which is so characteristic for the sepioid suborder, is recognizable only as a reminiscence in the forms described here (see the bottom row of Textfig. 59, and Textfig. 140). In the Gulf of Naples, we indeed find only sepiids and sepiolids, in both of which the shell formation and its relation to the soft body are atypically specialized; whereas the embryonic development of spirulids and idiosepiids, which are in many respects closer to the archetypal form, is still

unknown. But even in the families mentioned the embryos have an ample shell sac in special forms! Whereas the sepiid shell sac produces a variant of the sepioid shell whose relation to the archetype is still recognizable via intermediary forms (fossils),
 199 the sepiolid shell sac provides at least by its primary size and shape some indications (Textfig. 100) for the past existence of a truly sepioid cuttlebone.

Of course the amplitude of the shell sac in sepioids is related to its original destination to accommodate a chambered shell, whereas the thin plate of a teuthoid gladius requires only a slit-shaped space. The two families are complementary to one another in that the sepiolid shell represents the part that has been lost almost completely in the sepiids, namely the proostracum; this fact is already reflected at early stages (Pl. 23, Fig. 1) by the shape of the shell sac (Textfig. 100 a: Vs).

These conditions, viewed in comparison with those of the fossil sepioids and of a juvenile *Spirula* (Textfig. 85), and with those of the related teuthoids and belemnoids, indeed led us to our ideas about the typical features of the suborder (Textfig. 59). The arguments put forward are visualized in Textfigure 85. (see also Vol. 1, pp. 473-504) Here we have to apply these ideas to the earlier embryonic stages of shell development and to the establishment of its relationships with the mantle sac, justifying the ideal stages defined in Textfigure 59 (bottom row).

This can be done best using a hypothetical construction of *Spirula* development, which in turn provides an opportunity to validate our morphological principles (cf. pp. 79-82). There is indeed no doubt that the inferences made here can later be tested by actual observations.



Textfigure 85. — Juvenile stages of different sepioids, in schematic representation (from Vol. 1, p. 477).

- a) *Spirula spirula* (after preserved specimen).
- b) *Spirulirostra bellardii* (reconstructed from fossil shell nucleus).
- c) *Belosepia sepioidea* (idem).
- d) *Sepia orbignyana* (after preserved specimen).

The typical juvenile conditions of this group of forms are represented by *Spirulirostra* (b); the shell is drawn too strongly curved in the diagram, which figures the membranous and muscular mantle as transparent. Note that the muscular mantle inserts on the outer surface of the phragmocone.

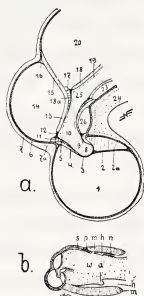
2. On the Embryonic Development of *Spirula*

Real embryonic stages of *Spirula* have not been found to date, or have at any rate not been described. However, Pelseneer has already provided in 1895 (Huxley and Pelseneer) a hypothetical construction of the phases of shell and mantle development in this "living fossil", and his idea has subsequently been taken over in more recent literature (cf. Joubin, 1920 and Prell, 1922). Although Pelseneer has high merits for his elucidation of molluscan morphology, he has made an unfortunate mistake here. Despite its shell, *Spirula* is not a living fossil in the sense of a closer relation to the ectocochleates; it merely conserves structures which are primary and typical for all dibranchiates, decapods, and sepioids, and which have been lost in other representatives of these groups in quite different ways. Only in the closely related sepiids are corresponding parts still in existence; these parts have been so strongly modified in the sepiids, however, that it proved rather difficult to recognize the morphological relation (cf. Vol. 1, pp. 433-501). Textfigure 85 provides a picture of our understanding as far as the most advanced embryonic and early postembryonic stages are concerned. The following points have to be emphasized:

In all dibranchiates, the shell is definitely internal, the primary shell epithelium becomes completely covered by the shell sac fold at an early state, even before the shell begins to be formed, so the shell sac is entirely closed (Textfig. 43). There is no reason to infer for *Spirula* something different from what is known from all its close and remote relatives. Early closure of the shell sac must be a very ancient feature, as demonstrated by the huge rostral sheaths of the atraktites, the oldest known dibranchiates, from upper paleozoic strata.

The shell of *Spirula* must be formed inside a shell sac, and its first rudiment (p. 119), if still exposed, must become covered by the secondary shell epithelium. This is demonstrated by the relatively thick sheath layer on the initial chamber (Textfig. 86 a). A different question is that about the correlation between the early shell and the soft parts: can it be thought of as corresponding to typical sepioid conditions (Textfig. 85) from the outset? Anything else would indeed result in a highly abnormal formation of the posterior end so long as the initial chamber is less than a 3/4 closed sphere, i.e. roughly a hemisphere. Thus the only conceivable insertion of the early shell in the mantle sac is that shown in Textfigures 55 and 71, which provides us with a link to the typical developmental stages of all dibranchiates. We have indeed to suppose that the

early stages of the shell and its relation to the mantle correspond to the situation shown in Textfigure 43 and that its subsequent modification followed the course shown in Textfigure 59 (bottom), i.e. by a variation derived from the stages shown in Textfigure 55.



Textfigure 86. — Medial section (obtained by grinding) through the initial chamber of a *Spirula* shell (a), 32× natural size, and hypothetical medial section of the mantle sac of a mature embryo of *Spirula* (b), 4× natural size. — From Volume 1, page 512. —

a) This figure was prepared using Appellöf's (1893) indications, especially his Plate 9, Figure 1. — The primary shell wall (ostracum and hypostracum) is marked cross hatched (6), the periostracum (7) is dotted along with the septa and septal necks (18, 15, 13, 5, 4). Within the siphuncle, the epithelium of the soft body is marked by a dotted line. 1: initial chamber; 2: prosiphon (transverse stay); 2a: its sagittal lamella; 3: conchiolin cap as initial part of shell siphuncle; 4: calcified neck of the second septum; 14: second chamber; 15: second septum; 16: angular substance; 17: pillars of 3rd septal neck; 18: third septal neck; 19: siphuncular epithelium; 20: third gas chamber; 23: its ventral part; 24: ventral ridge of periostracum; 25: second septal swelling of siphuncle; 26: ventral part of second gas chamber.

b) As far as the stage of shell development at hatching is concerned, this figure is based on calculations made from the size of mature ovarian eggs, and considerations on the relationship between egg size and hatching size as observed in other decapods. In such a small animal, only a few of the shell components shown in Textfigure 84 can be lodged; a final relic of the proostracum (p) may in turn be present at that stage.

1: muscular mantle; 2: remainder of proostracum; 3: shell sac (shell epithelium).

Along with the progressive narrowing of the aperture of the 3/4 sphere, its free ventral and lateral margin becomes detached from the muscular mantle and thus comes to lie inside the sac (Textfig. 86 b). The question then is what happens to the dorsal edge. A similar process could occur in the early embryo, perhaps in a less atypical fashion, since a proostracum is lacking already in the young *Spirula* (Textfig. 84); indeed it must be lacking, because it could no longer be inserted in the typical fashion (since the dorsal mantle cavity has become expanded posteriorly beyond the shell rim,

so that the mantle muscle has been shifted onto the outside of the shell wall). But it is unlikely, indeed virtually against the rules according to our general experience, that so fundamental an element of organization should have disappeared altogether from early development, especially since the topographical conditions for its expression seem to exist prior to the above-mentioned modifications. We therefore believe that a proostracal rudiment similar to that shown in Textfigure 59 (bottom) exists in *Spirula* (Textfig. 86 b), at least as a part of the shell sac, but later lags behind the rest in development, so that the muscular mantle becomes fused in the dorsal midline and finally replaces the rudimentary dorsal plate. At the hatching stage, the proostracum (Textfig. 86 b) probably is very reduced, and the shift of muscular mantle insertion probably is underway on, the dorsal side as well.

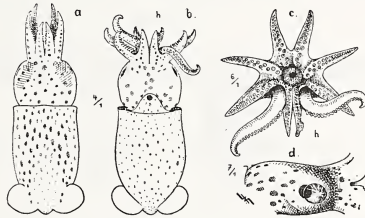
As to the general aspects of shell development by the time of hatching, we have some indications (cf. Vol. 1, p. 515 and explanations for Textfig. 86 b): probably there are two complete gas chambers which are accommodated in the mantle sac according to the typical sepioid mode (given the size conditions), so that this stage should look very similar to the condition shown in Textfigure 4. Since the shell curvature is not yet strong, the initial chamber does not yet lie virtually inside the mantle sac, and the ventral edge of the shell does not yet cut as deeply into the viscera as it will later on.

The external aspect can be imagined similar to Textfigure 85 a, differing from *Sepia* by the open primary lids, the weaker arms, and the lack of lateral edges on the ventral arms. The suckers of the sessile arms probably are arranged in 4 rows, those of the tentacles in at least 8 rows (cf. Pl. 21, Fig. 2).

3. On the Modification of the Sepioidea

The development of the fossil sepioids (belemnosids, belopterids, spirulirostrids, spirulirostrinids) should be derived from very similar stages, as far as the earliest parts of their shells can reveal. Among the extant forms, *Idiosepius* (Textfig. 87) is especially interesting in comparison to *Spirula*, on the one hand, and to the sepiolids (see there) on the other. The adult animal seems to be devoid of any shell remnant (similar to certain sepiolids); but the outline of the mantle sac with the small, subterminal, round fins shows a form which "suggests" (cf. Steenstrup, 1881) the earlier presence

of a *Spirula*-like shell (cf. also *Spirulirostridium*: Vol. 1, p. 495). At any rate, this animal is much closer to the typical sepioid than the related sepiolids, and since the embryos of the latter (Textfig. 100 a) show reminiscences of a once powerful sepioid cuttlebone, it seems likely that the embryos of *Idiosepius* show even more complete
 203 and more typically developed rudiments of past shell formation. An embryological study of this smallest of all cephalopods would be highly desirable, since it could provide important data for a better knowledge of the whole group.



Textfigure 87. — *Idiosepius paradoxus*, the smallest living cephalopod, at the adult stage; 4× natural size; — From Volume 1, page 503. — a) Dorsal view. b) Ventral view. c) Arm crown (male; h: hectocotylus), 6× natural size. d) Lateral view of head, 7× natural size.

Note shape and position of the fins, the mantle sac end and the mantle rim, and the tentacular arms with biserial suckers. The dorsal view shows an oval field of glandular (opaque) skin, in a position where normally the broader parts of a typical sepioid shell would be expected to lie. The ventral arms are hectocotylized. The primary lid is contracted to form a cornea, with wrinkles probably radiating from the pore. The latter is not recognizable, but is probably not closed entirely.

CHAPTER 9

The Embryonic Development of the Sepiids

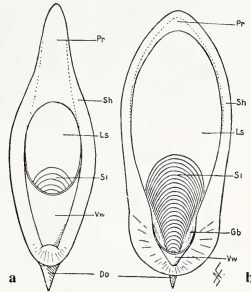
Contents: 1. Generalities. 2. *Sepia officinalis* (p. 216). 3. *Sepia elegans* (p. 242). 4. *Sepia orbignyana* (p. 243)

1. Generalities

Before going into details of embryonic development in sepiids, it will be useful to get a general idea about the systematic and phylogenetic relationship of this family with other sepioids (vol. 1, pp. 517-522). This relationship can now be assessed based on the cuttlebone, which is a peculiar variant of the general sepioid type that can be viewed along with a series of fossil forms. The closest among the latter is represented by the genus *Spirulirostrina* (vol. 1, p. 501), which has to be mentioned here first. Next to it we place a hypothetical transitional form called "*Spirulisepia*" (vol. 1, p. 520) and further away the fossil *Belosepia*; however, this fossil form in its overall aspect already resembles the present-day type of the sepiidae (subfamily Sepiinae) so that we can put it aside for the moment (but see Textfigs. 85 and 94 a about the aspect of the shell nucleus).

Thus we compare the hypothetical *Spirulisepia* cuttlebone directly with that of living sepiids, the latter being represented by the typical conditions (with a short siphuncular part) of juvenile *Sepia officinalis* (cf. Vol. 1, p. 550). We consider *Spirulisepia* as having a mixture of (still) *Spirulirostra*—and (already) *Sepia*-like fea-

tures; something that actually is observable in *Spirulirostrina*, but with greater emphasis on the ancient features. The overall outline is of little importance in this context; the cuttlebone in Textfigure 88a is could be imagined more elongate, hence more similar to the *Spirulirostrina* bone (vol. 1, p. 501).



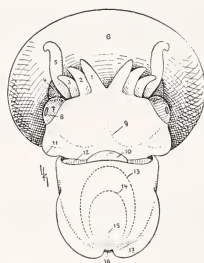
Textfigure 88. — Diagrams illustrating the derivation of a typical sepiid cuttlebone (b) from conditions such as those observed in *Spirulirostra* and *Spirulirostrina* via an ideal transitional form, *Spirulisepia* (a). In phylogenetic terms the latter is a hypothetical intermediary stage of the morphological series, which starts out from *Belemnosella* and (via the above-mentioned forms and *Belosepia*) leads to *Sepia* (cf. Vol. 1, pp. 481, 498, 501, 520).

Note the following traits, which are still *Spirulirostra*-like, in the transitional stage (left): 1) the very large rostrum (Do); 2) the "capitulum" lying next to it (which hides the initial chamber of the phragmocone); 3) the well preserved ventral wall (Vw) of the phragmocone; 4) the round shell aperture through which a wide siphuncle (si) is visible; 5) the formation of a short proostracrum (Pr); 6) the connection between the capitulum and the proostracrum by a broad lateral edge (Sh), which are connected with one another only posteriorly by other projecting parts (ventral process). — The following features are already similar to traits of *Sepia*: 1) the relative regression of the rostrum and capitulum; 2) the slanting position of the last septum; 3) the regression of the ventral wall. The further modification making this into a cuttlebone is illustrated by the figure b.

Of some importance for the understanding of sepiid organization are the following modifications of the primary sepioid type: 1) The prong of the sheath (periostracrum) is strongly reduced, but it can be conserved as a solid spine supporting the fleshy "terminal knob" of the mantle sac (Pl. 20). 2) The capital of the sheath, i.e. the protuberance on the ventral side which contains the initial chamber, flattens out with decreasing curvature of the latter. 3) The whole phragmocone loses its originally high vault and curvature (Textfigs. 85, 94) and becomes rather flat. 4) As a consequence the septa are increasingly slanting, the dorsal end reaching far forward. 5) The lateral

edges of the sheath participate in this movement and overtake the anterior shell rim, to embrace the degenerating proostracum.

Textfigure 89 illustrates the rather early expression of this modification in living sepiids; here again we do not find a complete recapitulation of the assumed ancestral series in the course of embryonic development (pp. 41, 78). The flattened initial chamber of the modified phragmocone is no longer in terminal position, but shifted dorsally, and the suture of the first septum already lies (stage XV) well beyond the middle part of the body. The cuttlebone thus formed shows the subfamily characters from the beginning, rather than typical features of the family or even the suborder.



Textfigure 89. — Embryo of *Sepia officinalis* at stage XVI. Outline drawn after living specimen. Details that are visible only in preserved specimens were added later (cf. Pl. 16). The inner organs (shining through the integument of a living embryo) are not shown.

1-4: sessile arms; 5: tentacle; 6: yolk sac; 7: eye ball; 8: iris; 9: posterior edge of head cover; 10: nuchal attachment; 11: cheek hump; 12: funnel pouch; 13: shell rim; 14: first suture line shining through the integument; 15: Hoyle's organ; 16: terminal knob; 17: fin.

Reminiscences of older, more general formations can at best be expected in certain species at very early stages (shape of the shell sac). One should nevertheless note the slightly pointed anterior end of the shell in Figure 4 of Plate 20; this represents a weak rudiment of the proostracum; it is not clearly visible in a merely translucent whole-embryo preparation. If the curvature of this embryonic cuttlebone were more marked, one could very well believe he saw an early stage of the type shown in Textfigure 88 a.

206 If the phylogeny of the genus *Sepia* is to be derived from the natural system as completely as possible, in the sense of Textfigure 3 as principally required (p. 31), then that natural system must be viewed in a more differentiated expression than was

done in Volume 1 (p. 810) where the more practical aspects of orderly representation of forms were emphasized: indeed a mere juxtaposition of sepioid families does not fully translate their systematic-morphological relationships. The highly special congruences of sepiids and spirulirostrinids in fact justify the formation of a distinct, specialised group (circle), the **Spirulirostroidea** already mentioned on page 32. This group can and must be systematically united with the spirulirostrids in a group called **Spirulirostroidea** (see again p. 32) which is distinct from other fossil sepioids. Whereas the spirulids are without any doubt members of this group, the position of the idiosepiids and sepiolids in such a system is still uncertain. Therefore this system is not proposed in the sense of a solid species catalog, but merely used here to express the special type position of *Sepia*. This position can be defined completely (as far as fossils can tell) by the following scheme of names:

<i>Amphioxus</i>	4. Coelomata
<i>Polygordius</i>	5. Eutrocheata
<i>Lepidopleurus</i>	6. Mollusca
<i>Fissurella</i>	7. Conchifera
<i>Nautilus</i>	8. Cephalopoda
<i>Octopus</i>	9. Dibranchiata
<i>Belemnites</i>	10. Decapoda
<i>Loligo</i>	11. Tentaculifera
<i>Belemnosella</i>	12. Sepioidea
<i>Spirulirostra</i>	13. Spirulirostroidea
<i>Spirulirostrina</i>	14. Spirulirostrinoidea
<i>Belosepia</i>	15. Sepiidae
<i>Hemisepius</i>	16. Sepiinae
	17. <i>Sepia</i>

For a better understanding, this scheme should be translated into the form of Textfigure 3, with the three outermost circles of that figure added.

Three species were available to me as representatives of sepiid development, with more or less complete series of embryonic stages: *Sepia officinalis*, *S. elegans*, and *S.*

orbignyana. Details of systematic-morphological importance relating to the latter two species will be discussed at the end of the chapter. There are no really major differences, and I therefore limit the description of development essentially to the most common species:

2. *Sepia officinalis*

The ripe eggs of this species are very large; in the common, smaller coastal form they generally measure 6×4.8 mm, sometimes a little less. In the large animals of deeper water I found that eggs measure about 7 mm in length.

Cleavage follows the decapod type described on page 146; but the 16 cell stage already shows a peculiarity: the cells derived from the upper, medial octomeres are generally not true micromeres; they remain in continuation with the periphery, although their center is shifted to the inner part of the germinal disk (Pl. 13, Fig. 3); they become divided into a macromere and a micromere by the following, centripetal cleavage step (cf. *Octopus*, Pl. 24, Fig. 9). From the 32 cell stage, heterochronies and irregularities occur frequently (cf. Pl. 13, Fig. 4).

But in principle the bauplan of the cleaved germinal disk is very similar to that of *Loligo* (Pl. 1). We find the central field of small cells (Pl. 13, Fig. 5: mf) and its narrow extension towards the lower border, which is called the "middle band" (mb), a simple ring of yolk cells (rz) and a soon to be irregular mosaic of micromeres which occupy the greater part of the blastodisc.

When the endomesoderm ring appears (Pl. 13, Fig. 6), the rim of the blastoderm is subdivided into fine lobes from each of which a plasmic strand radiates out. Each lobe contains a considerable number of cells (6-12), of which at least the peripheral yolk cells (p. 96) remain in continuity with the yolk and are determined to become constituents of the yolk epithelium. Once the endomesoderm ring has grown somewhat broader (Pl. 13, Fig. 7), a characteristic pattern appears: from below the ring with its circular outer border (which also marks the limit of the ectoderm), the now regularly shaped "rays" emerge. Each ray consists of a proximal, broader part in which the nuclei (light dots in the figure) are arranged in two rows, generally in alternating order. The outermost nucleus forms the base for the fine plasmic strand that radiates out on the yolk and dwindles away there.

These rays dissolve later to become single rows of rather isolated yolk cells (Pl. 14, Fig. 1) which decrease rapidly in number as they are drawn in under the germinal disk (Fig. 2). At stage II-III (Pl. 14, Fig. 3) they are absent altogether and they never reappear. During further growth of the blastodisc a thin yolk envelope (Pl. 14, Fig. 4) is differentiated from the periphery of the disc as in *Loligo*. The rest represents the body of the animal proper, the "embryonic body", which becomes further differentiated by organization of the mesoderm (Pl. 14, Figs. 4-7) as described earlier (pp. 103-107).

208 This state (Pl. 15, Fig. 1) is the preparation for the folding processes which start at stage VIII (Pl. 15, Fig. 2). The embryonic body is surrounded by the arm crown, which is interrupted only in the area of the mouth. The 10 bipartite arm rudiments are not quite identical: the first and third on either side are weaker than the others; the fourth rudiment, i.e. the tentacle, is not yet more conspicuous and looks like a normal arm rudiment. Even the ventral arms (V) are not markedly weaker (as in teuthoids) but are very similar to the tentacle rudiments. The cephalic anlagen and the statocysts do not show any special feature. As to the funnel apparatus, the funnel tube rudiments are very delicate and hazy, and they are not yet connected to the much more distinct funnel pouch rudiments; the latter are connected to each other by the ventral "belt strip" which is also more distinct than the funnel tube rudiments. Medially the funnel tube rudiments are in contact with the arm crown, from which they are not yet separated at stage VII (Pl. 15, Fig. 1) (cf. p. 105). The rudiment of the muscular mantle is a flat ring whose inner and outer rims are slightly elevated; in the medial line, both dorsally and (more markedly) ventrally, a distinct longitudinal depression is visible; its morphological significance is obscure. The edge surrounding the shell epithelium, i.e. the rudiment of the shell fold, is almost circular; it shows no sign of an anterior extension as in sepioids (Pl. 23, Fig. 1). This small difference is probably related to the fact that the sepiids have nearly or totally lost the prostracum.

Stage IX (Pl. 15, Fig. 3; Pl. 17, Fig. 1) shows the bipartite nature of the less advanced arm rudiments as well. A striking feature is the great distance separating the first (I) arm rudiment from the others, which lie more ventrally in almost equal distances from one another. One should remember (pp. 105, 116) that the arm rudiments have already been shifted in relation to the head anlage. Pair I now lies well anteriorly to the eyes, Pair II comes close to the eyes; Pair III has passed the statocysts, while Pair IV comes close to them and will later pass them too (Pl. 13, Fig. 4). Needless to emphasize that the description of the early *Sepia* stages given by Kölliker (1844) are

very inaccurate and partly misleading. (See Lang 1900, pp. 450-451 on the subject: Textfig. 404 A lacks the arm crown and the parts given are a highly schematic, partial representation of my stage VIII, as figured here in Figure 2 of Plate 15. In Fig. 404 B the dorsal arms are missing, otherwise the same conditions obtain. 404 C corresponds roughly to my Figure 4 of Plate 15; these pictures are again very incomplete and partly misleading. The same is true for Figure 405.)

The inequality of individual arm development is still distinct at Stage IX. Moreover, the tentacles (IV) are now markedly predominant, whereas arm rudiment III appears as the weakest; this condition will persist for some time and is reminiscent of the teuthoids. Later on the three dorsal pairs will become more uniform (Pls. 19, 20), whereas the ventral pair grows larger than they.

The eye vesicles are almost closed; behind them an edge becomes visible (between x and z), which corresponds to the prospective position of the posterior connecting piece of the corneal fold. It cannot be considered the proper rudiment of the latter; it arises more incidentally as part of the depression between the eye (z) and the huge ectodermic growth. The latter, which was named cephalic plate by Kölliker, is the rudiment of the major part of the white body; it will later occupy the cheek area (cf. Pl. 15, Fig. 4: close to y).

The funnel tube rudiments now join the funnel pouches on either side, the statocyst is contracted, and the mantle rim has been extended posteriorly to cover the gills. The shell sac begins to close; the outside of the shell fold shows elevations which represent the fin rudiments. It looks as if the closure again followed three seams that remain visible as delicate furrows marking the future position of Hoyle's organ; this impression is enhanced when viewing the next stage. (See also Textfigs 36 and 37)

At stage X (Pl. 15, Fig. 4; Pl. 17, Fig. 2) the germinal disk is markedly contracted, and the relief of the embryo is more distinct than before. This process was preceded by the full enclosure of the yolk in the yolk sac envelope, and it looks as if this were a prerequisite for the opposite shift of the embryo proper. Nevertheless, in the apical view chosen, all the arm rudiments are still visible, whereas at later stages the further contraction of the arm crown will pull them underneath the embryonic body. They still show the primary, bipartite structure, which however, begins to fade progressively. The third arm rudiment is still the weakest on either side, the fourth (tn) is stronger than the other rudiments. The mouth has become smaller, the eye vesicles are closed completely. Close to the eye, additional furrows appear between the elevations

of the white body (y), in a way similar to what happens in *Loligo*; the optic ganglia and the cerebral ganglia, which are derived from the same complex of anlagen (p. 108), are already situated at a deeper level. The cerebral ganglia remain nevertheless recognizable in the hazy spots (x) situated above the foremost parts of the funnel pouch rudiments, where they can still be seen in figures of Plate 16.

The funnel apparatus, which does not yet show the rudiment of the nuchal cartilage, begins to shift beneath the mantle rim, which it has approached in the course of
 210 the general contraction. The funnel retractors are very distinct (Textfig. 38).

The mantle rudiment has become bowl-shaped; its apex still shows the open shell sac pore from which the three "seams" radiate. The round elevations flanking the lateral seams are distinct rudiments of the fins. It is already clear that they have an unusual size (cf. Pls. 2 and 121), which corresponds to the strong development of the fins in *Sepia*. Whereas normally such an enlargement starts from a small, terminal juvenile fin (Pl. 7), the definitive state here encroaches upon the earliest rudiment. However, we will see that even in *Sepia* the fin undergoes a secondary enlargement and a shift of its anterior end of insertion; thus the rudiment is a terminal one in spite of its considerable size, as can be seen from its positional relationship with the shell pore (cf. Pls. 16-18). The gills show only their tips in the overall aspect; they have become elongate appendices, showing the typical flattening and first hints of gill lamellae (Pl. 17, Fig. 2).

Stage XI (Pl. 15, Fig. 5; Pl. 17, Fig. 3) is past the major folding events: the embryo has pulled its arms under the head, the dorsal arms lying now close to the mouth. On the eye balls a delicate circular ridge forms the iris fold rudiment (ir) around the entirely closed pore of the vesicle, while on the head anlage the position of the posterior connecting piece of the prospective corneal fold becomes faintly visible. The funnel apparatus is already shifted below the mantle rim; dorsally it shows a first delimitation of the future nuchal attachment (nk). Other parts are recognizable only in a ventral aspect (Pl. 17): the funnel tube lobes (tr) grow towards each other and bend inwards. A delicate pit marks the position of the anus (an), behind which a low ridge extends to the mantle. This ridge is the rudiment of the mantle septum (ms). The gill rudiments (km) are differentiated: the two marginal edges are distinct; between them the gill lamellae form as alternating little folds, 3-4 on each side. Each arm rudiment shows a bluntly truncate end, and a shallow gutter along its outer side; along the inner side is a similar gutter, from which a low longitudinal ridge (x) arises. The latter is

already subdivided by transversal furrows at its proximal end; the resulting transverse elevations (cf. Pl. 21, Fig. 4) are the sucker rudiments.

The transition to stage XII is shown in Figure 1 of Plate 16 and in Figure 4 of Plate 17: a dorsal view shows the elongation of the arm rudiments which curve outwards. At their bases the arm pillars (pf₁, pf₂) arise and make contact with the head; the inner sides show the development of sucker rudiments as described above. The arm crown as a whole becomes further constricted, the dorsal arms closely applied to the
 211 mouth. The eyes show the iris fold more elevated, and the organization of the whole cephalic anlage becomes more clearly structured. The faint edge (x), which has been shown to mark the position of the posterior connecting piece of the corneal fold, now becomes more distinct.

The mantle rudiment is still broader than long; in lateral aspect, more than the posterior one half is occupied by the fins, which are not exactly lateral, but slightly dorsal. They are connected to each other by Hoyle's organ. The funnel pouches and the nuchal attachment begin to fit inside the mantle rim.

A ventral view (Pl. 17, Fig. 4) shows the voluminous cheek hump on each eye stalk. The arm pillars are also visible in this view, and especially the formation of the funnel tube is clearly visible. The tips of the gills are still sticking out from the mantle cavity; the latter already shows the most general features of its definitive organization.

Stage XII shows very clearly the primary differentiation of the arms (Pl. 16, Fig. 4). The tentacles are grown and hook-shaped, showing a strikingly long, single file of sucker rudiments, which is then further enlarged from the provisional tip. Proximally the more rounded sucker rudiments are already crowded and arranged in a zigzag pattern. The other arms, which will have to form a lower number of suckers, are much shorter; the growing tip shows the undifferentiated sucker ridge, and proximally the future zigzag arrangement of sucker rudiments is barely recognizable.

Here we see quite obviously the reminiscence of a phylogenetically preceding stage (Textfig. 28) with suckers arranged in single file, whereas the form of the sucker rudiment is an even more remote reminiscence, namely of tetrabranchiates, in which the suckers were represented by simple adhesive papillae similar to what exists in living *Nautilus*. Of course only the pattern of their rudiment is conserved here, whereas the finished structure is *replaced* by the true sucker.

Stage XII (Pl. 16, Fig. 2; Pl. 17, Figs. 5 and 6) completes the embryonic body in other respects as well. Remember the above statements. The posterior connecting

piece of the corneal fold (hb) now rises as a distinct, delicate ridge. A ventral view (Pl. 17) shows the increasing fusion of the funnel lobes along a seam (nt) progressing posteriorly, and the first, low papilla-shaped rudiments of the funnel attachments (kn) on the outside of the funnel corners. The mantle cavity is now much deeper and the funnel retractors form prominent longitudinal ridges inserted on the shell sac, slightly dorsally from the gills; the stellate ganglia are recognizable in a more laterodorsal position, forming round epithelial protuberances on the inner surface of the mantle. Further dorsally the mantle cavity is limited to the most anterior part of the mantle sac. The gills still extend freely from the body, without any relation to the mantle. Their two edges are distinct and prominent; between them (ventrally) lies a row of 5-6 gill lamellae. From the tip more lamellae are added rapidly. Between the gills, the anal papilla shows a pit between two labial elevations (i.e. an anterior and a posterior, ventral lip), which marks the place of the future surface opening of the intestine. Behind this future anal zone lies the ridge of the septum palli, and, visible through the skin of the visceral mass, the branchial hearts, their coelomic pouches and, further anteriorly (before the anal pit) the vena cava.

The transition to stage XII is characterized (Pl. 16, Fig. 3) by the progressive anchoring of the dorsal arm bases on the head, forming the so-called arm pillars. Such embryos already show a pear-shaped yolk sac, the pointed end of which carries the embryo proper; the latter is typically bent in relation to the axis of the yolk sac, which thus is slightly compressed. The crouched position of the embryo (cf. Textfig. 58) in the swollen chorion is characteristic (p. 148).

At stage XIII (Pl. 16, Fig. 5) the arm pillars, which are now fusing with one another, are progressing across the head surface; the third arm pillar is no longer individually distinguishable. The posterior end of the lateral edge facing the eye comes to lie in a slight depression, which relates it to the already existing posterior connecting piece of the corneal fold. The path of the migrating formation thus is determined in a way similar to what we have seen in *Loligo* (p. 168), where it appears more clearly on the ventral side, however. Otherwise the dorsal view does not exhibit any important feature: the arms have grown slightly in length; the area of the prospective nuchal attachment begins to become distinct.

In ventral view (Pl. 17, Figs. 7, 8) the funnel now appears as an entirely closed tube; the seam disappears at this stage; the posterior rim of the whole funnel apparatus is inserted in the mantle sac. The fused arm pillars of each side progress

posteriorly on the head surface; the posterior end (v) of the ocular edge now becomes firmly anchored. At the base of the tentacles a sharp constriction appears on either side, which prepares the later formation of the tentacle pouches; the constriction site indeed becomes invaginated. Moreover the distinction between the tentacular stalk and club, which appeared progressively during the preceding stages, is now very marked (Fig. 7).—Incidentally, a close examination of Pl. 21 shows that there is no basic difference between the tentacles and the normal arms: the latter also show a proximal part devoid of suckers, which is merely shorter and thicker than in the tentacle.—At the base of the tentacular club the double file arrangement of the suckers already grades into the pattern with four rows, whereas a double file arrangement is achieved on the arms.

When removing the ventral mantle wall, one obtains the aspect shown in Figure 8 213 of Pl. 17: the funnel attachments are distinct as shallow depressions. The gills now show 10-11 filaments on the ventral side, and the outer edge is forming a special connection to the mantle via a basal fold, which is the rudiment of the branchial attachment (kb). The anal papilla shows the papillar rudiments of the prospective "valves" flanking the edges of the slit.

When approaching stage XIV (Pl. 17, Fig. 9) the posterior end of the ocular edge (v) gets very close to the corresponding end of the posterior connecting piece (hb) on either side, following the path already mentioned for the preceding stage. The final connection can be best observed in the dorsal aspect (Pl. 16, Fig. 6). The intervening part of the primary cephalic surface is compressed (y) and separates for a short time the folds approaching each other, until it becomes cut as it were (Fig. 7).—Note that the primary cephalic epithelium falls into two parts, one of which becomes engulfed in the orbital cavity, and the other which continues to cover the posterior part of the head. In dorsal view the latter is subdivided into an apical and a lateral ("cheek") field by the oblique furrow running from the eye to the funnel apparatus. The apical field is largely conserved, whereas the cheek surface will undergo some further reduction to be described later.—At this stage the mouth (at z) is completely covered by the joined dorsal arms; the nuchal cartilage begins to become distinct. The shell sac contains a very delicate, broadly oval shell lamella, which is slightly calcified in its middle part only.

At stage XV (Pl. 16, Fig. 7; Pl. 17, Figs. 10 and 11) the corneal fold is closed. In a dorsal view a slight depression (at d) marks the position at which the lateral edge and

the posterior connecting piece made contact with one another. Further modifications of the head shape now begin: the eye stalks now are short, massive protuberances on which the eyes are oriented more anteriorly. The head covers become wider by progressively replacing the "frontal field" (marked by the position of the "x"). The posterior border of the head covers (y) reach the oblique furrow mentioned above and thus become directly connected to the cheek area; in the zone marked x it will come closer to the nuchal attachment.

The arm sucker rudiments become arranged in four rows (Pl. 21, Figs. 1 and 6), those of the tentacles in eight rows (Pl. 21, Fig. 8), and both arms and tentacles grow further in length. However, in both of them the terminal tip, which is particularly long and always curved outward in the tentacles, continues to exhibit the primary conditions, namely a longitudinal rib with transverse grooves which grades more proximally into a single file, then 2 to 4 files of closely packed sucker rudiments.

At this stage the nuchal attachment becomes much more distinct. It is strikingly broad, which corresponds to the primitive state as well as to the secondarily broad shell of cuttlefish. The shape of the nuchal attachment is roughly that of a quadrangular plate with arched anterior and posterior ends. The medial longitudinal rib is recognizable as a bright strip.

214 The mantle sac is strongly enlarged in combination with a marked widening of the inner cavities (mantle cavity, intestine, coelome, heart, branchial hearts) and special differentiation of the organs. In this process the fins have also grown larger and extend more anteriorly so that they now occupy the greater part of the lateral mantle surface. At the posterior end, the fins are not in direct contact with one another. Between them a contractile knob (es) exists which marks the position of the prospective spine of the cuttlebone. It represents the posterior end of the animal even though it may still lie slightly anterior to the bulging ventral part of the mantle. At this stage the first chromatophores appear.

A ventral view (Pl. 17, Figs. 1 and 11) shows the very important enlargement of the head covers, which have reached the cheek zone and thus reduce the primary head integument quite drastically. The incipient invagination of the tentacle base is more markedly visible now. The ventral arms now exhibit a typical sepiid formation, the lateral seams (ss). These are the longitudinal edges of the ventrolateral arm surfaces which proximally (y) grade into the head covers; they should not be mistaken for the normal outer edges of the decapodan ventral arms, which do exist here as well (Pl. 18,

Fig. 3) and continue into the edges of the tentacle pouches and form a connection with the lateroventral arms.

Dissection of the mantle exhibits the condition represented in Figure 11 of Plate 17: the funnel apparatus is largely finished; the funnel attachments are well developed as oval depressions, slightly pointed posteriorly. The anal papilla shows the typical quadripartite inflorescence pattern. The gills have made great progress in development: there are 13-15 gill lamellae on the ventral side. These lamellae are finely crimped, thus preparing the differentiation of second order lamellae. The gill attachments (kb) are markedly lengthened anteriorly, i.e. no longer so strictly proximal as they were at their earliest stage.

The integumental translucency allows one to recognize the branchial hearts and their appendages (pd) and coelomic pouches, the vena cava branches (vs), the venae palliales posteriores, the aorta posterior, the vena cava (vc) and the liver tubules (Cf. Pl. 18, Fig. 3). On either side of and slightly posterior to the anus the kidney papillae (still without a pore) are visible.

The buccal field requires a closer examination (Pl. 21, Fig. 1). First observation: the ventral arms are now much longer and stronger than the other sessile arms, and—more important—the rudiment of the buccal arm crown (“buccal funnel”) is now visible between the arm crown and the (cut) yolk sac base, which represents the oral area. This rudiment comprises 8 papillar elevations (bt₁-bt₈), each of which is associated with one particular arm rudiment. The ventral ones appear somewhat earlier and are recognizable from stage XIII (Pl. 17, Fig. 8). If we number these formations in the way we give numbers to the prehensile arms, i.e. starting from the dorsal side, then the first and second are situated at the bases of arms I and II, the third and fourth close to the bases of arms III and IV; the first two are somewhat shifted upwards, the other two somewhat downwards so that a wider gap appears between the second and third buccal arm rudiment. The first and second one are connected by a delicate ridge; from the third buccal arm two ridges start out dorsally and ventrally but they do not reach the second and the fourth buccal arm rudiment.

The general aspect of this arrangement conveys the impression of a buccal arm crown from which several elements have disappeared: the second rudiment lies between arms I and II, the third rudiment between arms III and IV, the first and the fourth rudiments between the dorsal and ventral arms, respectively. One is tempted to suppose a buccal arm rudiment between arms II and III, and another one at the base of

the tentacle, so that a buccal arm crown with 12 elements would obtain—something which I indeed infer for the earliest dibranchiates (cf. Textfig. 28). Such an inference cannot be proved at present as no other known decapod (*Rossia?*) shows these rudiments so early and in such a distinct, large form as it appears in *Sepia*.

The dorsal and ventral buccal arm rudiments are medially close to each other, but they do not yet tend to fuse. This is particularly clear for the dorsal rudiments: the mouth lies in the midline immediately beneath them; thus the mouth has migrated downwards not only between the dorsal arms, as we already know, but also between the dorsal buccal arm rudiments to take its definitive position. This is noteworthy because these rudiments will soon fuse together to form an unpaired medial structure (Pl. 21, Fig. 2); since the migration of the buccal complex is a prerequisite, this unpaired condition cannot be the primary state. Note also the earliest signs of tentacle pouch formation in the form of shallow depressions at the base of the tentacle stalk; it will soon become deeper.

This indeed happens already by stage XVI (Pl. 21, Fig. 2). As a consequence of the general arm crown contraction, a closed buccal arm crown anlage is soon achieved: the 8 papillae become connected by a low, circular ridge, and the two dorsal rudiments fuse into one single element (bt_1); thus the mouth (μ) disappears in a narrow slit. A much more advanced stage (Pl. 21, Fig. 3) is of special interest here, because it shows the exceptional condition (observed in only one other instance) where the dorsal buccal arm rudiments remain separate so that a circle with 8 buccal lappets would have formed if the embryo had pursued its development.

The shell sac at stage XV contains a broadly oval, slightly curved cuttlebone without chambers; it is still far from the stage shown in Figure 4 of Plate 20. Its broadest part is in the posterior one quarter, from which the lateral edges are almost parallel anteriorly before they converge in the anterior one third to achieve an outline comparable to the above-mentioned figure. The posterior rim is broadly curved, with a dish-like brim turned outward in the plane of the shell opening, as seems to be typical for cuttlebones (Textfig. 88). A marginal rim, which is broader anteriorly, is perfectly transparent being devoid of calcification (Pl. 20, Fig. 4), whereas the larger central area appears opaque and is brittle. In hydrochloric acid it shows effervescence and thus must be solidly calcified. The inner face shows bristle-like elevations in its deeper section; these are the pillars on which the first septum will soon come to rest (cf. Textfig. 95).

This juvenile shell contains an ostracum, a hypostracum and a periostracum, but these parts cannot be clearly distinguished.

At stage XVI (Pl. 16, Figs. 8 and 9) there is normally a buccal arm crown rudiment with 7 elements, as mentioned above, and the slit-shaped mouth (*mu*) is situated below the fused dorsal rudiment. The arm rudiments are essentially complete, and the tentacular club has 8 rows of suckers except on the growing tip. The club is so stretched, however, that these rows could be considered as 4 rows in zigzag crowding. (Imagine Fig. 8 of Pl. 21 after stretching in length) The tentacle pouches are already very distinct (Pl. 21). —On the head, the corneal fold is now contracted so that only the eye proper is exposed, not its surroundings. The head covers have grown in surface. Their posterior limit is recognizable in the dorsal aspect (Pl. 16, Fig. 9) where the apical field is further reduced, and also is visible as a delicate transverse furrow in the ventral aspect (Fig. 8). In the ventral aspect the olfactory tubercles (*ro*) become distinct on the hump-shaped cheeks.

The mantle sac is also further differentiated: the rim now forms a characteristic curve, with a mediodorsal convexity where a slight indentation was visible at earlier stages; likewise ventrally there are convex outlines on either side of the funnel tube. This results in a shallow, broad bay with a strait middle part (flanked by short straight, slanting lines) accommodating the funnel. This line is conserved and further differentiated during subsequent stages (Pls. 19 and 20) and in the adult.—The fin rudiments now show a characteristic form: they are not a uniform margin; one can easily see that their major development is in the posterior part, whereas the anterior part tapers off. This is the typical form of the fin growing forward on the mantle side; in *Sepia* it persists throughout later embryonic development (Pls. 18-20) and will be only slightly modified during postembryonic development. (See the figures in Volume 1, pp. 559, 557, 548) But the length and width of the fins will increase, in both absolute and relative terms, during the further course of embryonic development, as shown in the figures.—The terminal tip of the mantle sac and the outer limit of the nuchal attachment, which forms a delicate peripheral edge, become increasingly distinct at this stage, and the number of chromatophores is already very considerable; they are more closely placed on the mantle than on the head and arms; on the head they are still limited to the former arm pillars which have become the “head covers”, i.e. to the parts lying at the surface as in *Nautilus* (Textfig. 49).

The mantle sac has changed since the previous stage by forming what we may call

a "ventral shield", something that also appears in very similar form in the sepiolids (Vol. 1, p. 578). It is due to a slight flattening of the ventral mantle surface, flanked by two inconspicuous edges, the "lateral lines", which appear lighter than the surrounding parts. They are devoid of chromatophores, whereas the shield proper bears a limited number of weakly colored chromatophores; outside the lateral lines the chromatophores are densely set and strongly colored. This ventral differentiation shows its function soon after hatching: the young animals attach themselves to a hard substrate by applying the flat ventral surface to it. The lateral edges then become rather broad rims and thus increase the adhesive surface which functions much like a sucker. This apparatus is completed by the lower surfaces of the ventral arms, their swimming membranes acting like the lateral edges of the ventral mantle surface. (See Naef, 1926, *Zool. Jahrb. (Anat.)*, Vol. 48, p. 412)

This stage shows an embryonic cuttlebone which can be seen through the dorsal mantle skin in the living animal, as indicated by Textfigure 89. The first septum is formed, closing the shallow, subterminal embryonic chamber, which is not yet air-filled. (The outline is not correctly given in the above-mentioned figure, as can be seen from Textfigure 95, where the parabolically pointed anterior end appears more clearly. This detail is not of course easily recognizable through a translucent surface)

Stage XVII (Pl. 18, Figs. 1-3) shows an embryo, the body volume of which is roughly equal to the volume of the yolk sac. The base of the latter now shows (at least in preserved specimens) a distinct annular constriction close to the mouth. This is the site of an annular muscle that drives yolk into the embryo proper, later on permitting the total autotomy of the yolk sac. To avoid this, one has to be very careful when handling embryos for fixation of whole specimens. From this stage on, an embryo can develop further without the yolk sac, and with great care such an individual can be reared to become a viable animal. See the closing chapter for the interesting observations that I was able to make on such "premature" hatchlings.

218 The brachial apparatus is essentially finished: at the arm tips the formation of new sucker rudiments has nearly come to an end; it continues at a very slow pace with few rudiments added. The same is true in the tentacles: the club has become relatively shorter, and the suckers are arranged in exactly 8 rows except at the base and tip. Sometimes a delicate edge appears already on either side along the surface occupied by the suckers; this border is the rudiment of the "protective membrane". The outermost end of the tentacular club remains devoid of suckers up to the adult stage and

thus forms the "terminal knob". On the arms there are 4 very regular rows of small suckers or sucker rudiments, on either side of which a distinct edge forms the rudiment of the protective membrane and thus limits the inner side of the arm. The tentacle pouch has continued to grow deeper (Pl. 21).

The typical heptameric buccal membrane surrounds the conserved root of the yolk sac, which has been dropped (in the specimen figured) and now forms a slightly bulging field, in the center of which the round scar (na) of the amputation site is visible.

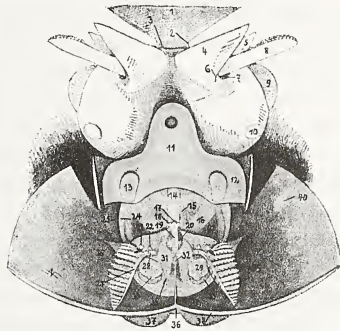
The ventral arm now has more strongly developed lateral rims, the insertion of which is now more proximal on the head. Along the outer faces of the remaining arms the delicate glandular lines reach distinctly backwards on the head, almost as far as the head covers. The latter have reduced the frontal field into a narrow zone (y) lying before the nuchal cartilage (Pl. 18, Fig. 1). The corneal fold has grown into a primary lid (pl), which is able to contract over the eye in response to certain stimuli, in other words is functional and no longer a mere rudiment. The olfactory tubercle on the ventral cheek zone has further contracted itself and thus attained the typical embryonic form.

The mantle sac appears markedly enlarged in relation to the head. In some details certain differentiations are notable: the terminal tip (cf. Textfigs. 89, 93) generally does not show up in a ventral view, because the ventral surface of the mantle bulges posteriorly and thus hides it. In other states of contraction the picture changes, however (Pl. 18, Fig. 2): the muscular mantle is pulled forward and reveals the terminal tip as a medial connection between the fins, forming a sort of frenulum with the mantle end in a way very similar to what occurs in some oegopsids (cf. Vol. 1, pp. 344, 355, 359, 365, and Textfig. 41 on p. 116).

Dissection of the mantle cavity and funnel apparatus shows a situation (Pl. 18, Fig. 3) that is typical for young decapods: the funnel tube and the funnel pouches (tt) are subdivided by a pair of projecting walls, the funnel septa (ts), on each of which a funnel retractor (rt) is inserted. The funnel pouches occupy the mantle entrance like a collar. Inside the funnel tube, the A-shaped medial part is the funnel gland (td), the crescent-shaped valve membrane more anteriorly is the funnel valve (kl). Behind the funnel gland the vena cava (vc) arises from two roots (the cephalic veins); several lateral branches are recognizable on either side of the vena before it reaches the level of the anus (an). The anal papilla is now clearly composed of the 4 typical parts (p. 139).

From it the intestine reaches backwards and partly covers the small, pear-shaped ink sac (tb), which is still situated in strictly medial alignment, i.e. in a perfectly typical position. On either side of the intestine, the two kidney papillae (np) are visible; their surface pores are not yet distinctly open. Their outline grades into the anterior mantle furrow, which on each side reaches the base of the gill.

The gills are definitively shaped as far as their essential features are concerned: the first order gill lamellae have generated second order lamellae on the crests of the earlier pleats (Pl. 17), which results in a fern-like aspect. The gill attachment bank (ks)



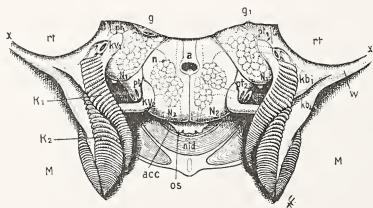
Textfigure 90. — Mantle cavity of a *Sepia officinalis* embryo at stage XVII (Pl. 18, Fig. 3) cut open and pulled out in such a way that an arrangement of the parts as close to *Nautilus* as possible is obtained, permitting a direct comparison with Textfigure 91 (same as Textfig. 11). 13× natural size.

Both figures show: 1) anterior and posterior mantle furrow as limits of the mantle roof complex, on either side of which the gills are situated; 2) the paired gills, only the larger, posterior pair of *Nautilus* being represented in *Sepia* (the archetypal position of the lacking pair is marked by small, black feather patterns below the genital pores); 3) the relationship of the head-foot retractor (rt) with the gill base; in *Sepia* this retractor is represented by the funnel retractor; 4) the transparent kidney sac allows the posterior vein branches with their appendages to be seen (31) and to recognize their positional relation to the afferent and efferent branchial vessels and to the anus.

1: yolk sac; 2: yolk stalk; 3: buccal funnel; 4: ventral arm; 5: lateral arm; 6 outer edge of ventral arm; 7: tentacle pouch at the outset of invagination; 8: tentacular arm; 9: eye ball; 10: olfactory tubercle; 11: funnel tube (seam); 12: funnel pouch; 13: funnel attachment; 14: Vena cava; 15: Nervus visceralis; 16: liver; 17: anus, upper lip; 18: anal wings; 19: hindgut; 20: ink sac, still small and situated medially; 21: upper mantle furrow; 22: kidney pore; 23: genital pore (rudiment of spermatophoric or oviducal gland); 24: funnel retractor; 25: stellate ganglion; 26: branchial band; 27: branchial vein; 28: "auricle"; 29: branchial heart; 30: pericardial gland; 31: vein branch with grape-like appendages; 32: central heart with Aorta posterior; 33: coelom pouch containing the branchial heart; 34: mantle septum; 35: Vena pallialis posterior, position of prospective nidamental gland rudiments; 36: terminal tubercle; 37: fin; 38: muscular mantle, cut apart; 39: inner mantle surface; 40: mantle attachment.

has grown further forward, as has the medial mantle septum (ps) with the arteria pallialis media (am) lying in its anterior edge. Of the large, superficial veins of the ventral side, the venae palliales laterales (vl) are now visible in addition to the venae palliales posteriores (vp), and alongside the latter the arteriae palliales posteriores; Ap is the Aorta posterior. Due to the translucent epidermis the following organs also can be seen: the branchial hearts (kh) with their appendages (Vpd) and the limitation of their coelomic pouches (x), the two cephalic vein branches with the grape-like venous appendages, the Aorta posterior (ap) which appears behind the transversal limitation of the kidney sacs. The bright, slanting bands (lb) between the anus and the gills are the paired liver rudiments. When the gills are turned back (Textfig. 90) a light-colored epithelial thickening becomes visible close to the base of the gill (at 23), slightly above and beyond the spot (22) where the primary rudiments of the kidney papillae should be located. The thickening is the rudiment of the outer sexual organ and the ectodermic part of the duct. It still marks the prospective genital pore.

Let us now use the typical mantle cavity features of this stage, which shows many primary traits and which can easily be related to the earlier stages, for a comparison with the corresponding parts of the fully developed *Nautilus*. (It would of course be more instructive if we could use a homologous stage of *Nautilus*, but unfortunately that is not yet possible). To make an understanding easier, we arrange the parts of a dissected *Sepia* in a situation (Textfig. 90) comparable to a *Nautilus* after appropriate manipulation (Textfig. 91). This will permit also a comparison of finer details and topographical relationships, in a way similar to what was done in Textfigures 22 and 29. The interpretation represented by the latter should now be confirmed by a demonstration of the strict applicability of that interpretation.



Textfigure 91. — Mantle cavity roof and neighboring parts (severed "abdominal complex") of a young female *Nautilus pompilius*, flattened out. For a detailed description see Textfigure 11 (p. 57).

220 Above all other things, we now have to consider the existence and shaping of a zone which we named the mantle cavity roof of the molluscs (p. 55); in virtually all representatives this zone is limited by an anterior and a posterior mantle furrow. In *Nautilus* the latter corresponds only incompletely to that of dibranchiates, because it is anterior to the nidamental glands; these lie in the mantle roof of dibranchiates (Textfig. 56) but are shifted to the mantle proper in *Nautilus*. On the other hand, the anus lies in the medial zone of the mantle cavity roof in *Nautilus*, whereas in the dibranchiates the anus is secondarily shifted to its anterior border and thus is pushed
221 beyond the ink sac and anterior mantle furrow. Comparison with Plate 17, however, demonstrates the secondary nature of this positional relationship.

Right and left are the gills, 2 pairs in *Nautilus*, 1 pair in *Sepia*. Given its relation to the other parts, the single pair of the latter can only be homologous to the posterior (lower) pair of *Nautilus* gills, as I have shown in 1913; this implies a very thorough correspondence of correlations involving the cephalic vein branches (31) with the venous appendages, the branchial nerves, the renal sacs, the anal area (as a whole: 19, 20), the posterior mantle vessels (39), the afferent and efferent branchial vessels and their chiasma, the pericardial glands (30), as well as the renal issue and pericardial funnel.

The last-mentioned formations can only be used in this comparison if they are considered in the position which is typical for cephalopods, i.e. that observed in *Nautilus* and in the octopods; it is from that position that they are secondarily shifted towards the anus in the decapods (Naef, 1913, p. 441). For our comparison, the renal pore (22) is shown in its archetypal position in Figure 90.

Whereas in *Nautilus* the organ complex connected to the gill base is metamericallly repeated, namely in the antero-lateral corners of the mantle cavity roof, in a sharply demarcated zone (which is roughly circumscribed in the left part of Textfigure 91 by the letters g, pt1, kv1, N1), the corresponding part in dibranchiates forms only one element of the anterior metamer, namely the sexual duct (23) that is homonomous to the renal pore, in a certainly very clear representation.

This situation can only be interpreted in phylogenetic terms by supposing that an anterior segment of the "abdominal complex" originally lying in the mantle cavity roof has been completely reduced in *Sepia* as well as in all the other dibranchiates. Such a process was possible since the organs of the anterior segment were functional-
222 ly replaceable by the organs of the posterior segment, which are more strongly

developed in *Nautilus* and probably were so in all the tetrabranchiates. The only element that was irreplaceable was the coelomic duct of the anterior metamer which is highly specialized as the sexual duct in all cephalopods (similar to the placophores, but unlike the molluscan and even the conchiferan archetypes); this duct lies behind an ectodermic, glandular section. The latter is represented by its rudiment (23) in Textfigure 90.

This glandular section should be related to any rudiment that could be homologous to the anterior gill of *Nautilus*; such an anterior gill rudiment would have to be situated where a small black feather is added to the figure, in a position corresponding exactly to the second pair of *Nautilus* gills. This would even confirm my earlier consideration (Naef, 1913) according to which the position of the sexual pore in *Nautilus* had undergone a shift from the gill base in anal direction, in a way similar to what obtains in the decapods: the rudiment of the sexual pore probably lies where the anterior gill base of *Nautilus* is situated, i.e. still far from the anterior mantle furrow and from the anus.

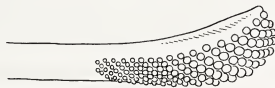
The Textfigures 90 and 91 of course are meant to be mutually elucidating; the peculiar features of *Nautilus*, which must be much closer to the archetype at least in terms of rudiments, are nevertheless more easily understandable when considering the more familiar condition of the dibranchiate embryo in relation to ontogenetically primary formations. Among these, the limited extent of the gill attachment (26) is striking; the fold indeed is limited to the gill base and leaves most of the gill free. Conversely, likely secondary complications of the dibranchiates are: 1) development of an ink sac in association with the shifted anus, 2) development of a branchial heart in the afferent branchial vessel, 3) development of a mantle septum providing a shorter route for the arteria pallialis posterior, 4) development of a branchial spleen in a fleshy (cf. *Nautilus*) gill axis (See Textfig. 68), 5) the whole arrangement of the mantle cavity roof in relation to the body; in *Nautilus* it reaches posteriorly along with the mantle, as hinted by the arrangement chosen for the preparation in Textfigure 90.

At this stage the first air chamber begins to merit its designation; instead of its gelatinous-fluid contents, some gas appears in the form of irregular bubbles squeezed between the pillars; it will finally fill the whole space of the chamber. But this will not be achieved before closure of the second chamber (now in preparation; see p. 227), which in turn will be without air at the beginning.

By stage XVIII (Pl. 18, Figs. 4 and 5; cf. Pl. 19, Fig. 4, Pl. 22, Fig. 1) considerable changes have occurred, which reflect a general specialization of the organization, with an expression of particular features of *Sepia*. The large swimming membranes of the ventral arms are particularly striking; the corneal fold contracts; it opens more widely than shown in the figure only when completely relaxed. The tentacle bases begin to form the tentacle pouches which are typical for this family: this is achieved by an increasing retroflexion of the tentacle stalk base in the already existing depression (Pls. 21, 22); a similar, but much less pronounced process is observable in the development of other decapods (cf. Vol. 1, p. 258, Textfig. 257). Thus the pouch is forcibly extended (cf. final section); this is possible since it lies immediately below the skin which is very extensible in all cephalopods; during the subsequent stages this situation will become increasingly marked. During these processes the tentacle stalk grows considerably in length.

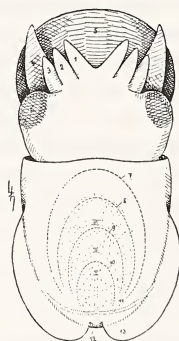
The club has also undergone modifications (Textfig. 92) that result in a form which is typical for sepioid development; the rims along the inner surface carrying the suckers have become more or less distinct (Pl. 18) thus indicating the beginning formation of protective membranes. Above the dorsal edge, which is curved slightly inward to the ventral side, we find a second edge which is nearly parallel to the former, but more strongly developed: this is the rudiment of the swimming membrane. The three edges fade away at the terminal knob. The surface carrying the suckers has also changed: it is markedly broader distally thus forming a manus; however, this broadening is not symmetrical, and this irregularity is indeed typical for the sepioids: the ventral edge grows longer than the dorsal one and thus curves downwards, in contrast to the opposite curvature of the dorsal edge.

This shape influences the formation and arrangement of the sucker rudiments: on the broader part of the club the sucker rudiments grow larger, whereas they appear



Textfigure 92. — Tentacular club of an embryo of *Sepia officinalis* at stage XVIII. — $46\times$ natural size. Note the generally valid distinction between the tentacular stalk and club, the proximal (carpal) part and the "manus" of the club, the swimming membrane and the terminal knob; note also the stretching of the longitudinal rows of sucker rudiments due to the bending of the ventral side of the manus. The overall shape and the pattern of sucker enlargement is still quite different from the adult condition (Vol. 1, p. 536, Pl. 7), but typical for sepioids.

reduced in size due to the shaping of the originally flat papillae, each of which becomes a small sphere sitting on a narrow base. Due to the unequal growth of the manus the sucker rudiments are also shifted around so that the originally 8 rows become irregular: the ventral marginal rows are extended due to the lengthening of the curved edge, the transverse rows are deformed as oblique curves, which are crossing with one another in 2 systems. The original arrangement of 8 rows is basically conserved, but the suckers of the ventral marginal rows of course must penetrate more deeply into the stretched gaps of the neighboring rows to achieve a regular distribution, so that zigzag rows of double and finally triple sucker numbers obtain; their origin is recognizable in principle, but the details are often difficult to analyse in the different sepioids.



Textfigure 93. — Living embryo of *Sepia officinalis* at stage XVIII-XIX. — 9× natural size. Normal attitude of the animal. The orbital cavities (6) are almost entirely closed (See Pl. 19, Fig. 5). The shell (7) shines through the dorsal skin. Note the 3 air chambers, the last one of which (III) still contains a gelatinous fluid in the live animal, although the septum is entirely closed.
1-4: arms; 5: yolk sac; 11: Hoyle's organ; 12: terminal tubercle; 13: fin.

Dissection of the mantle cavity reveals all the parts to be enlarged and differentiated: 1) the hindgut and ink sac begin a rotation around an imaginary common axis, the hindgut being moved to the left side, the ink sac to the opposite side. This rotation continues and leads to the situation of the ink sac which comes to lie medially close to the surface, just below the ventral integument (Pl. 19), the rectum being pushed laterally and downwards in its more posterior section. Thus the basic condition for a fur-

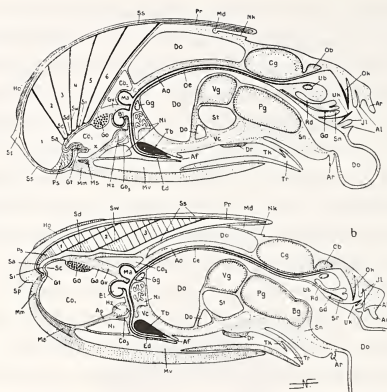
ther postembryonic shift is achieved. 2) In female individuals, the rudiments of the nidamental glands (nd) appear in their typical position, where the venae palliales posteriores emerge from the kidney sac (Pl. 18, Fig. 4). They consist of an annular concentration of mesoderm cells, forming a slight elevation of the thickened epithelium and thus preparing an annular fold, which will later contract to form a small sac (Pls. 19 and 20).

During the subsequent transitional stages these processes show a rapid progress (Textfig. 93; Pl. 19, Figs. 4 and 5; Pl. 22, Fig. 1): the tentacle pouches become
 225 enlarged, so that the coiled tentacles are completely hidden in them unless they are stretched out. The buccal funnel grows in height all around, the 7 supports being only slightly in advance compared to the connecting velar membranes (Pl. 22). The corneal
 226 fold progressively contracts definitively; close to the remaining pore the secondary lid fold becomes prominent (Pl. 19, Fig. 5). However, this is visible only when the musculature of the primary lid contracts (Pl. 19, Fig. 6); the rim then becomes pleated, and the periphery of the pore and its anterior edge reach out ventrally to form a fold that covers the free edge. This fold becomes progressively distinct and finally persists even without any contraction.

Thus the secondary lid fold in its turn forms itself based on a functional condition that becomes fixed; the only prerequisites being the extensibility of the corneal fold and the existence of a circular musculature close to the opening. In the sepiids this opening is definitely included in the secondary lid, which becomes distinct before the former is contracted into a delicate pore. During the same period the iris fold edge is transformed into the shape typical for the sepiids (Pl. 19, Figs. 5 and 7), and the olfactory tubercle is differentiated in the way typical for the Sepioidea: its marginal zone becomes elevated to form an annular ridge while the sensory epithelium is lowered to form a pit. The whole organ remains a prominent structure, however, so it cannot be considered the result of an initial invagination (Pl. 19, Figs. 4 and 5).

The cuttlebones of these stages are of particular interest (Pl. 20, Figs. 4-6; Textfig. 95). For their systematic-morphological orientation see pp. 213-214.

The embryonic cuttlebone (Pl. 20, Fig. 4), the normal position of which can be seen in Textfig. 94 b, is viewed from the concave side; it is already of limited depth. The outer margin could be simply called conotheca rim, although here the conotheca is no longer distinct, but integrated into a layer that must be interpreted as the sheath (periostracum). It is therefore more appropriate to designate the thin main plate of the whole as the "dorsal shield".



Textfigure 94. — Medial sections of advanced sepiid embryos (stage XVIII). — From Volume 1, pages 524. — $12\times$ natural size.

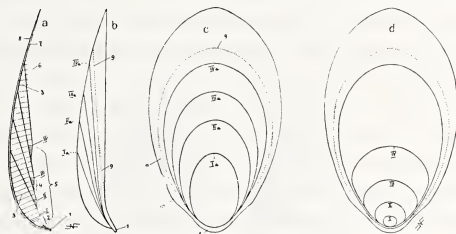
b) Schematic medial section of an embryo of *Sepia officinalis* illustrating the cuttlebone and its correlation with the soft body. The conotheca and the periostracum, which together form the "dorsal shield", unfortunately cannot be clearly distinguished. The rear end shows a hint of the prominent part called fork (Gt). See the much more completely differentiated formation in a. In the air chambers (1-3) one can see the "pillars", which are represented by simple lines, note especially those representing the prosiphon (Ps) and the depression in the first septum (Sa), which represents the initial caecum of the siphuncle, being followed by the homologa of the septal necks (Sd). The rostrum is still lacking.

a) Construction of a corresponding section of an embryo of the fossil *Belosepia*, based on the known shell nucleus (cf. Vol. 1, pp. 521 and 523). The prosiphon, the siphuncle, and the air chambers are here even more normal and thus illustrate the atypical condition of b. A rather well-developed proostracal rudiment (Pr) can be assumed. The yolk sac (Do) is arbitrarily reduced in size (simply to show it entirely). — For further explanations see Textfigures 55, 63 and 84.

Af: anus; Al: outer lip; Ao: Aorta anterior; Ap: Aorta posterior; Ar: buccal arm rudiments (buccal funnel); Bl: caecum; C6-10: coelome sections; Cg: cerebral ganglion; Do: yolk; Dr: funnel gland; Ed: hindgut; Ga: genital arteries; Gd: poison gland; Gg: Ganglion gastricum; Go: gonad; Gv: genital vein; Gt: fork of the cuttlebone; Ho: Hoyle's organ; Hz: heart; Jl: inner lip; Ma: stomach; Md: dorsal mantle cavity; Mv: ventral mantle cavity; Mm: muscular mantle; Ms: mantle septum; Ni: kidney sac; Nk: nuchal attachment; Ob: upper buccal ganglion; Oe: oesophagus; Ok: upper beak; Pg: pedal ganglion; Pr: proostracum; Ps: siphuncular coelom; Sd: septal neck; So: fleshy siphuncle; Sn: subradular organ; Sp: terminal tubercle of mantle sac; Ss: shell sac; St: statocyst; Sw: shell septum; Tb: ink sac; Tk: funnel valve; Tr: funnel tube; Ub: lower buccal ganglion; Uk: lower beak; Vc: Vena cava; Vg: visceral ganglion; x: ventral rim of conotheca.

This dorsal shield is fully transparent (dark on a black background), flexible and uncalcified (p. 225) in its marginal part, which is broader anteriorly; this condition persists during later growth stages. The larger (middle and posterior) part appears whitish and is rather strongly calcified, especially the thickened, everted posterior

rim; the latter is a phylogenetically quite interesting part of the dorsal shield named the ventral process (Vol. 1, pp. 500, 522). The neighboring lateral broadenings, which are more distinct at younger stages (p. 224), also correspond to special parts of extinct sepioids, namely to the lateral wings or lateral edges (Vol. 1, figures on pages 492, 494, 497, 498, 501), but taper out anteriorly without any distinct border. The parabolic pointing at the anterior end is the last reminiscence of a proostracum.



Textfigure 95. — Embryonic shell of *Sepia officinalis* with 4 air chambers (stage XVIII-XIX). 10× natural size. Semi-schematic representation (cf. Pl. 20, Fig. 4).

a) Medial section. 1: ventral process; 2: initial part of siphuncle; 3: first and fourth chamber, with pillars; 4: part representing the siphuncular neck of the third septum; 5: siphuncular depression of the fourth septum; 6: pillars for the fifth septum; 7: conotheca in the proostracal part; 8: periostracum (dorsal shield). — b) Lateral view, 9: limit of calcified parts; 10: suture lines. — c) Dorsal view, 10: corners between lateral edge and "ventral process". — d) Ventral view. I-IV: siphuncular parts of the 4 septa. Anteriorly a very rudimentary proostracum.

227 The part marked by light dots (Pl. 20, Fig. 4) is the chambered section of the shell, the greater anterior portion being covered by the last formed, third shell septum, which shows an overall smooth, oval suture line. The underlying second septum can be seen by transparency, whereas the anterior part of the first septum is no longer recognizable across the subsequent septa.—Posteriorly each septum grades into a finely dotted strip which represents the septal neck. The latter is very wide in the third septum, so that the shallow siphuncular depression allows one to see the second and first septal necks. The first septal neck is a circular pit situated at the posterior, ventral rim of the phragmocone. The siphuncular necks 2 and 3 join the first and second septum, respectively, leaving only a narrow strip of them uncovered.

This situation is illustrated in Textfigure 95, especially in the medial section (a), which shows a somewhat more advanced stage with 4 chambers but is otherwise very

similar. Here one sees the reason behind the white dots of the plate figures: they represent the pillars which support the septa and which (at 6) already are formed in preparation for the fifth septum. These structures are delicate rods that are flattened, as it were, so that their insertion, especially the distal one, is not a point but a short (always curved) line. Later on, these structures are aligned longitudinally, and their supporting lines form delicate, meandering strips at the lower surface of each septum (Vol. 1, p. 532).

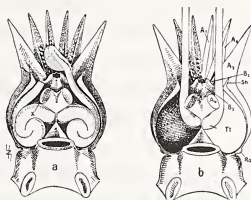
228 Stage XIX (Pl. 19, Figs. 1, 3; Pl. 22, Figs. 2, 4) is a young *Sepia* with a still sizable yolk sac, but otherwise almost completely developed, i.e. in a state that permits survival outside the egg envelopes without special care. The arms are completely differentiated, and the larger sucker rudiments have become functional due to the invagination of the suction chamber. At rest the tentacles are completely hidden in the tentacle pouches. The buccal funnel is further differentiated: on its outer surface the supports form prominent ridges, which proximally begin to connect to the arm bases by delicate skin folds. These so-called buccal funnel attachments are perfectly visible on Plate 22 (Fig. 2): the dorsal attachment terminates between the two dorsal arms, connected to them by low muscular strands. The second attachment reaches to the base of the second arm where the upper protective membrane starts, whereas the third and fourth attachment each extend to the lower protective membrane of the third and fourth arm, respectively, without being very closely connected to them. These attachments subdivide the circular, slit-like depression separating the buccal funnel from the arm crown into six portions, which will be called buccal pouches. (They are often called "water pores", an indeed misleading designation.) They are particularly conspicuous in the most advanced stage (Pl. 22, Fig. 3). (See also Textfig. 83).

The arms, including those of the third and fourth pair, are connected to one another by distinct velar skin folds. At the entrance to the tentacle pouches (Pl. 21), these folds are particularly developed (Pl. 22). They are broader there and their stronger musculature enables them to contract strongly thus hiding the tentacles almost entirely.

On the head the eyes are now much enlarged and shifted laterally from the former eye stalk complex, something that occurs only during postembryonic stages in the teuthoids, while the cheek complex has grown very inconspicuous (cf. Vol. 1, figures on pp. 306 and 319). The eye lids are now completely formed, as shown in Figure 7 of Plate 19. The orbital pore is barely visible; the secondary lid fold (sl) is crescent-

shaped and surrounds the roughly W-shaped pupil (pu) which is covered by a smooth, tough, transparent cornea; the latter remains elastic and does not wrinkle when the circular musculature of the secondary lid contracts.

In a ventral view of the head, the retracted tentacles at rest are recognizable: each forms a very characteristic coil, which will be more complicated in the adult animal (Textfig. 96). When the tentacle is fully retracted, the club is bent inwards like the blade of a folding knife (Pl. 19, Fig. 1: tk), so that only the outer face of the carpal part is visible in the tentacle pouch opening (Pl. 22, Fig. 2). It is only during the preparation of tentacle ejection that the tip of the club is brought forward (Pl. 22, Fig. 3).



Textfigure 96. — Preparation illustrating the fully formed tentacle pouches in *Sepia elegans*. Ventral arms (A₁) and funnel tube removed. Pouches entirely exposed.

a) Tentacular stalks coiled in typical fashion inside the pouches, right club removed, left club pulled forward. Note the relation of the tentacle base (Ti) to the axis of the ventral arms, the formation of the connecting band (x), the shape of the club.

b) Tentacles pulled entirely forward, thus emptying the tentacle pouches. Note the narrow pouch opening, which is limited by the thick web connection (Sh) between the third and fourth arm. Ro: olfactory organ B₁, B₂: buccal pillars; A₁-4: arms.

229 The olfactory organs (ro) are shifted more laterally and backwards to take up their typical definitive position. A dorsal view reveals some inner organs, which appear separated by slight depressions and are recognizable through the integument, namely the buccal mass and the cerebral ganglia behind it, more laterally the white bodies which embed the optic ganglia. Anterior to the nuchal attachment, there is still a narrow strip devoid of chromatophores, which corresponds to the "apical field" of earlier embryos. Elsewhere chromatophores are now numerous, except in some characteristic areas which remain devoid of them, namely the ventral surface of the fins, the major part of the funnel apparatus (which shows only a few chromatophores on its lateral parts), the cornea, etc. On the ventral mantle surface, the ventral shield and the lateral ridges (sl) are very distinct; laterally from the ridges a series of light spots (wx) appears on either

side; these spots can be erected as papillae. They are the forerunners of the later skin papillation, each (variable) papilla being generated by a special complex of muscle fibers whose contraction forces the otherwise smooth skin surface to rise up (Pl. 19).

The mantle cavity shows no new differentiations; the existing ones are merely differentiated further and enhanced (Pl. 19, Fig. 3). The ink sac has continued its rotation; the nidamental glands are now pit-shaped depressions.

Stage XX represents the newly-hatched animal with a completely reduced yolk sac (Pl. 20, Figs. 1-3, 5, 6; Pl. 22, Figs. 3, 7); apart from the sexual organs it is very similar to the adult in most respects, including the whole physiological condition.

230 The buccal field of a somewhat older, postembryonic stage is figured in the already described Plate 22 (Fig. 3); note the 7 buccal pillars (1-4), lappets and attachments (a-d), the relation of the latter to the protective membranes of the arms, moreover the 6 surrounding buccal pouches (I-III), the protective and velar membranes of the arms, the tentacle pouch entrances (7) from which the tips of the tentacular clubs emerge (8).

A closer inspection is necessary to understand the differentiation of the mouth, which occurs in parallel with the reduction of the yolk sac during the stages XIX and XX. If during stage XIX the yolk sac is cut off (at na) along with a portion of the buccal funnel, then we obtain the picture of Fig. 4 (Pl. 22), which is easily compared to Fig. 1: the buccal rim is enlarged and now exposes a swollen skin fold (il), the so-called inner lip, surrounding the tip of the lower beak.

During the subsequent, transitional stages (Figs. 5 and 6), this process becomes increasingly pronounced; it corresponds essentially to what is observed in all the dibranchiates. The expanding primary buccal rim becomes differentiated as the outer lip; it finally replaces the superficial part of the inner yolk organ while the yolk sac proper shrinks away. Clearly, the inner lip is formed from a rudiment lying inside the stomodaeum; it reaches the surface only secondarily (cf. Textfigs. 94 and 84). At postembryonic stages the tips of the beaks (Pl. 22, Fig. 4), the radula and the subradular organ can also protrude from the mouth. This occurs during feeding, especially during the extraction of flesh from bivalve and crab shells.

Plate 20 (Fig. 2) shows the arms in their typical position when the young animal points at a prey (*Mysis*) located in front of it, about one to two body lengths away. The arms are then held in a cone-shaped complex from which the tips of the tentacular clubs emerge, before they are ejected in a flash. Note the strongly protracted swimming membranes between the dorsal arms and the broad edges of the ventral arms.

The head shows no major modifications, whereas the mantle has continued to grow in relative size, with increasing differentiation of its parts. The mantle rim is shaped in the above-mentioned manner (p. 226), the fins are much larger and broader than before, but they remain separated by the terminal tip posteriorly. Along the fin insertion on the mantle, a further series of transient skin papillae appears, while smaller papillae are scattered on the dorsal surface. Hoyle's organ is still distinct immediately after hatching, but it disappears rapidly afterwards without leaving a trace.

231 The ventral side shows the flat mantle shield, sharply bordered by the lateral ridges. The latter can flatten out, or can be raised as sharp edges or narrow folds. When the animal sits on a flat bottom (e.g. in a glass vessel), the ventral shield is closely applied to the substrate and thus forms an effective surface of adhesion. The latter is enhanced by the lateral ridges or folds, so that the skin musculature acts like a flat sucker. The ventral arms, with their ventral surfaces enlarged by the lateral edges, participate in this action. Thus the young animals (like the adults) cannot only bury in sand by a combination of jetting and fin movements, they can also attach themselves to hard substrates (rock), protecting themselves by color and form mimicry, namely using chromatophore patterns and skin papillation.

The chromatophores can be distinguished, especially on the mantle shield, as dark, brownish ones and light, orange-yellow ones; the pattern is essentially dominated by the former. Outside the lateral ridges they are darker and more densely set than inside, and their distribution and hue are far from regular; there are light gaps where papillae can be formed. The functioning of the chromatophores is controlled in a way to have a common innervation for certain complexes, in multiple combinations allowing the generation of stereotyped patterns, which cannot be described here in detail. For example, the line between the apical part and the arm bases is such a stereotyped feature of the pattern (Pl. 20, Fig. 2).

The mantle cavity (Pl. 20, Fig. 3) exhibits essentially the features already visible during the two preceding stages. The ink sac is strongly enlarged and entirely shifted ventrally; it now lies in the median lines, its posterior end reaching the anterior edge of the septum palliale, and grows on towards the arteria pallialis medialis. The latter will soon be pushed to the left side. The nidamental glands are contracted to form small sacs. In the figure the gills are in their typical position, their tips being directed to the inner opening of the funnel (into which they reach under normal life conditions). They are still largely free; the gill attachment being limited to barely more than one half of their length. Laterally in the gill axis a light structure is visible, the so-

called branchial spleen, to which the first order gill lamellae are attached by tiny skin folds. The second order lamellae are more clearly visible now.

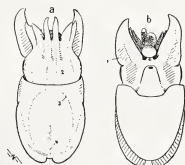
The cuttlebone of the newly-hatched animal is figured on Plate 20 (Figs. 5, 6). There is no longer any trace of a proostracum in the anterior end; in contrast, the free lateral edges of the dorsal shield have grown broader, especially in the posterior portion, and calcification here reaches the outermost edge; finally the lateral edges converge suddenly and grade into a very different, grained, rough part of the shield edge, which can be considered the homolog of the ventral process of *Spirulirostra* (p. 235).

The shell septa or "hump lamellae" have reached a number of 8 (7-8), essentially retaining the features described earlier. Only the siphuncular openings are increasingly large in the newly-formed septa; in the common form of *Sepia officinalis* at Naples (cf. Vol. 1, p. 550), the surface of the last siphuncular openings already is larger than the surface of the corresponding septa. In this context, the differentiation of the part called the fork becomes less distinct: in a whole-mount preparation, it is no longer possible to clearly distinguish the individual septal necks in this portion, although it seems clear that each septum adds a new lamella to the fork. The latter begins to rise as a sharp edge at the posterior end of the phragmocone and thus forms the ventral wall of it (cf. Vol. 1, Textfig. 308). In a dorsal view of the living animal, the phragmocone as a whole shines through the integument when the chromatophores are contracted; the insertion lines of the septa with their typical excentric contours are still distinct, providing a hint of the archetypal ventral curvature (Textfig. 94). At the posterior end of the phragmocone, the rudiment of the rostrum appears as a small, rather pointed tip.

3. *Sepia elegans*

The eggs of this species are much smaller than those of *S. officinalis* (cf. p. 71); but both the form and the structure of the envelopes are closely similar to those of *S. officinalis*. However, they are never observed in large clusters. Jatta (1896, p. 159, Pl. 2, Fig. 47; Pl. 7, Fig. 17) figured these eggs believing they were those of *S. orbignyana*; to recognize the error it is sufficient to dissect the ovary of a mature female of either one of these two species. I have not seen any striking difference from

S. officinalis in the surface development of the embryos of this species; at later stages, however, the chromatophores are yellow-brown rather than the dark sepia brown, and the ventral arms are particularly long at relatively early stages already, whereas the fins are shorter than at comparable stages of *S. officinalis*, as can be seen in the figure of a mature embryo (Textfig. 97). In particular, however, the number of suckers on the arms and tentacular clubs are much less numerous, and those of the arms are not arranged in 4 rows but in two simple or zigzag lines (cf. Vol. 1, p. 561).



Textfigure 97. — Mature embryos of *Sepia elegans*, newly hatched. 5 x natural size. — From Volume 1, page 563. In the dorsal view (a) note the still short fins, the cuttlebone (3) shining through the skin, Hoyle's organ (4), the nearly straight mantle rim, the dorsal arms connected by strong webs, the very long ventral arms with the broad lateral edges. 2: glandular lines.

The ventral view (b) shows the remaining small yolk sac, surrounded by the buccal funnel. — See also Jatta, 1896, Plate 7, Figure 21!

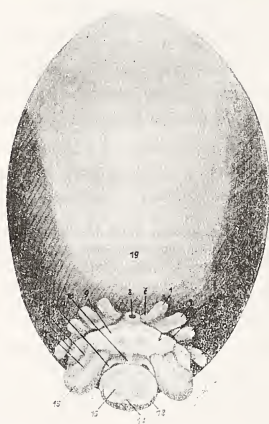
In contrast to *S. officinalis*, the embryonic shell of *S. elegans* shows a peculiarity which it shares with a number of other species including *S. orbignyana*: the siphuncular depression no longer has a circular outline (which would be an archetypal reminiscence); instead the posterior rim of each septum is a barely curved line, which does not embrace the siphuncular part. (cf. Vol. 1, pp. 550 and 563 for the juvenile cuttlebones). The parts homologous to the septal necks thus are nearly straight, transverse stripes on the hump. In *S. elegans* the absence of a rostral spine moreover underlines the derived character of the shell (loc. cit.).

4. *Sepia orbignyana*

The eggs of this species were described as those of *S. elegans* by Jatta (1896, p. 164; Pl. 8, Figs. 7, 8). They are found embedded in sponges and are devoid of the

typical gelatinous capsule of other sepoid eggs; the chorion in turn is especially tough*. Their shape also is striking: they are elongate and measure about 4.5×7.2 mm.

This egg shape is reflected by the form of the yolk sac, which shows characteristic differences from *S. officinalis* at all stages (Textfig. 98). The early embryo is situated at the apex of the long oval yolk mass, shifted only slightly to the dorsal side. At later stages this shift is expressed increasingly (Pl. 19, Fig. 7) by the appearance of a medial indentation of the posterior surface of the yolk sac below the embryo.



Textfigure 98. — Embryo of *Sepia orbignyana* at stage XI. $13\times$ natural size. See Plate 15, Figure 5 to assess the general similarity, slight heterochronies notwithstanding. Note the positional relationship between the embryo proper and the yolk sac (19) and the shape of the latter, which deviates from the norm. The furrows on the outer arm faces, resulting from a double rudiment formation (Pl. 15), and the broadly blunt ends of the arms are conspicuous.

1-4: arms; 5: tentacular arm; 6: limiting furrow between the arms and the head; 7: process directed towards the mouth; 8: mouth; 9: cerebral ganglion, shining through the surface; 10: position of the nuchal attachment; 11: funnel pouch; 12: limit between the eye vesicle and the ocular stalk; 13: iris; 14: primary lid fold, connecting piece; 15: cheek-hump; 16: mantle sac; 17: shell sac pore, or the scar remaining after its closure; 18: fin.

*Scientific Editor: this is an observational error; the chorion is surrounded by tightly wrapped gelatinous envelopes.

For the differentiation of the surface organization, the above description of *S. elegans* is valid: deviations from the patterns observed in *S. officinalis* are inconspicuous, rather difficult to describe. Of interest are some heterochronies: thus Textfig. 98 shows the brachial apparatus and the buccal complex slightly more advanced than the corresponding stage of *S. officinalis* (Pl. 15, Fig. 5). In contrast, the iris fold rudiment is not yet distinct. More of these differences cannot be described here in detail.

The mature embryo is similar to that of *S. elegans*. As in the latter, the darker chromatophores are yellowish- to reddish-brown, lighter than in *S. officinalis* (Pl. 19, Fig. 7). The early embryonic shell is also similar to that of *S. elegans*; the later embryonic shell, however, already has a robust spine (stage XX), more strongly developed
234 than in corresponding stages of *S. officinalis*. The late embryonic shell is strikingly broad, as is the juvenile shell (vol. 1, p. 559).

CHAPTER 10

The Embryonic Development of the Sepioids

Contents: 1. Generalities. 2. The typical embryonic development of the Sepiolineae (p. 247). 3. On the embryonic development of *Rossia* (p. 259). 4. On the embryonic development of the genus *Sepiola* (p. 260). 5. On the embryonic development of the genus *Sepietta* (p. 264). On the embryonic development of the genus *Rondeletiola* (p. 265).

1. Generalities

The embryonic development of sepioids is rather similar to that of sepiids; this is particularly important for the recognition of typical features in the Sepioidea, since there are, on the other hand, some differences between the two families that exclude a very close kinship. Thus it is likely that the common features are primary ones of the Sepioidea, since the adaptive specializations are rather divergent (cf. Vol. 1, p. 573).

About the similarity of the eggs and the general characteristics of development, see p. 203; subsequent sections deal also with typical early conditions of the germinal disk.

Our description can therefore start with the onset of folding processes, which offer a picture still very similar to that shown for *Sepia* (Pls. 15 and 23).

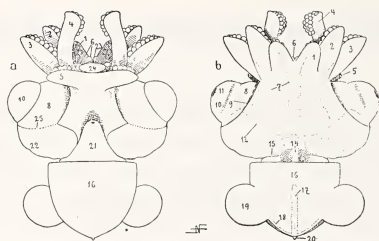
2. The Typical Embryonic Development of the Sepiolinae

The genus *Rossia* is clearly most representative of the archetypal condition of sepiolids. Since this genus has huge eggs, one can expect particularly well-sculptured surface aspects of the embryo, something that should make their study very interesting. Unfortunately no sufficient material was available to me, so our survey of sepiolid development will have to be limited to the species formerly lumped together as *Sepiola rondeleti*, in other words to the subfamily Sepiolinae.

Here again the available material was far from ideal, but above all else the available time and working effort were insufficient to exploit this material completely. Therefore no species is represented by a complete description of all the stages. However, the processes observed in different Sepiolinae are so similar that they are
 236 best combined in a common picture, the validity of which will be only slightly reduced when considering special cases.

Eggs occasionally are laid by Sepiolinae kept in aquaria, especially by those species living in the coastal area: *Sepietta obscura*, *Sepiola affinis* and *Sepiola rondeleti*, but also *Sepietta oweniana*. But I never obtained a great number of eggs developing normally; to achieve this, specially equipped aquaria would have to be set up, something I was unable to do given the various other tasks related to my work. On the other hand, eggs collected from the sea are often difficult to identify to species level, and the early embryonic stages are not sufficiently different in morphological terms to allow a distinction either. In contrast, the more advanced stages (following about stage X) show some specific differences in the individual development of the arms and other parts of the body (cf. Pl. 23, Fig. 6 and Textfig. 99); but above all else, the difference of size of the eggs and developing embryos and their yolk sacs allows one to distinguish species to a certain point at early stages, and at later stages (following stage XVII) the differentiation or the lack of luminous glands permits the distinction of *Sepiola* and *Sepietta*. But always some eggs cannot be identified, and the identification of others is sometimes doubtful. That is another reason for giving a generalized description.

It should be noted at the outset that this description also probably is valid for *Rossia*, with the exception of specifications that will be given further below, and



Textfigure 99. — Embryo of *Sepietta oweniana* at stage XIV-XV. 22× natural size. Living animal, after removal of the yolk sac. Slightly schematic representation. 1-5: arms; 6: buccal pillar rudiments; 7: glandular lines, ridge-like; 8: ocular stalk; 9: primary lid; 10: eye ball; 11: pupil; 12: posterior edge of head covers; 14: nuchal attachment; 15: funnel pouch; 16: mantle sac; 17, 18: Hoyle's organ; 19: fin; 20: terminal spine.

supposedly it is valid also for the systematically intermediary Heteroteuthinae, as far as their early developmental stages are not marked by secondary adaptations.

At first sight, stage VIII-IX shows only few notable differences from *Sepia* (Pl. 15): the 10 arm rudiments are developed rather equally, the dorsal ones only slightly less, the tentacles a little more strongly than the rest. The lower, unpaired rudiment is also clearly recognizable. Between arm rudiments I and II, the typical gap is visible on either side. The picture leaves no doubt about the homonomy of the 10 arms, both sessile and stalked ones (tentacles).

However, a closer comparison of correlations will show that the arm rudiments have already taken up a secondary position in relation to the other parts of the cephalopodium: the second pair lies halfway between the eye and the statocyst, whereas the third has already passed the statocyst. This corresponds to the lay-out of stage IX of *Sepia* (Pl. 15, Fig. 2), whereas the degree of differentiation of the individual rudiments corresponds to stage VIII (Pl. 15, Fig. 2). The shift of the rudiments appears to correspond to the situation in *Sepia*; when looking at younger stages, however, one finds the primary position of the parts observed in *Sepia*, but with much lesser distinctness of the rudiments. One can easily imagine how such a difference can be enhanced in the course of phylogenetic modifications; it would result in a developmental mode in which the primary bauplan (cf. p. 118) is no longer recognizable, as seems to happen frequently elsewhere.

On the other hand, the question remains whether in *Sepia* the primary location of the arm rudiments is really visible, or whether Figures 1 and 2 of Plate 15 mere-

ly show a phase of migration, whereas in Figure 7 of Plate 14, an even earlier phase is not recognizable. The question cannot be answered by simple observation; it probably could be resolved by an experimental approach (cf. final section of this volume).

The mantle rudiment shows the typical medial depressions in the upper and lower parts of the ring (y, z); more important, the shell sac rudiment shows a distinct corner (x) (cf. p. 226), which corresponds to the proostracum. It is not surprising that this formation is visible so early, since it is the only part of the shell that will be really differentiated, whereas the remaining shell sac represents a so-called "phylogenetic reminiscence". This does not of course say anything about the cause or the effect of its appearance; we will see in the description of the inner development that the shell sac parts not secreting an actual shell formation provide a transitory support for several other formations, which would be forced to find new developmental pathways (in other words, they would no longer be possible in the given form) if the corresponding parts of the shell sac rudiment were missing. This is what apparently obtains with regard to many "useless rudiments" that appear (without any other, visible necessity) in animal development. It is indeed striking that the shell sac rudiment shows nearly the same size as in *Sepia* where a shell is actually formed. The stage figured is probably from *Sepioloa ligulata* Naef; as is the following one.

Stage X (Plate 23, Figure 2) shows a markedly contracted germinal disk, resulting from the progressive folding processes. The distances between arm rudiments are even, and the rudiments themselves show a very characteristic form. The primary bipartite structure is still distinct; there are pairs of papillae marked by an indentation on the inner and outer side, respectively. These indentations of course correspond to the gutters observed in the *Sepia* arms; and here the indentations also will form gutters later on. In the outer one, a single (clearly premature) sucker rudiment (sn) is situated; each represents the first proximal sucker of an arm. On either side, the third and fourth arm rudiments are connected by a peculiar edge or rib (vb), which extends also to the second and fifth arm rudiments on the inner side. This is the rudiment of the anterior connection of the corneal fold, as can be seen later. Since the basal parts of the second and fifth arm rudiments are integrated, the fold can be considered as the
 238 anlage of the entire brachial part of the corneal fold; it is clear that the later differentiation of the actual arm pillars will simply push the existing edge on to the head surface. Thus the extremities of the edge can be considered homologous to the connected pillar rudiments, or the entire edge can be viewed as the connecting mass of the whole

arm crown, from which the anterior connecting piece generally can be derived (p. 126).

The edge of the mouth (mu) is very sharply differentiated. Between the eyes two small depressions (fe) appear; they correspond to the "windows" observed in *Loligo* embryos (p. 167; Pl. 2, Fig. 12). The statocysts (st) still exhibit the outer pore. The funnel rudiment (tr) shows the typical structure. In contrast, the mantle surface is more peculiar: from the shell sac pore (sp), four furrows depart, the three typical ones, which are rather indistinct, plus a fourth furrow which extends down and probably represents a transitory skin fold. The fins are set far from the pore, laterally, their edge directed backwards rather than upwards (cf. Pl. 15, Fig. 4). They are rounded lobes that are much more distinct than the corresponding structures of *Sepia* at the same stage.

Stage XI-XII (Pl. 23, Figs. 3 and 4) can be compared to the *Sepia* stages figured on Plates 15 (Fig. 5), 16 (Fig. 1) and 17 (Fig. 4). This specimen is from a different species than the preceding two; it (and the following) belongs to *Sepietta oweniana*, but it can be added here without any problem. However, the arm crown shows a disparity of arm rudiments, which appears typical for the genus, but which might occur also in certain species of *Sepiolo*: the ventral arms are only slightly, the dorsal arms strongly, retarded in relation to the others, as can be seen most clearly from the lower side of the embryo when it is removed from the yolk mass (Pl. 23, Fig. 4). All arms now have several papilliform sucker rudiments (the dorsal arms only 2); on the four lower arm pairs they are proximally arranged in a zigzag double row, whereas the 3-4 terminal sucker rudiments still form a single file. Subsequently 4 rows of suckers are formed in *Rossia*, as in *Sepia*. The longitudinal furrow on the outer arm surface remains visible, and on the tip is the last-formed sucker rudiment. The head shows a pattern of furrows and elevations that is very similar to *Sepia*.

On the mantle, there is a marked shift of the fins in anterior direction, so that the (still visible) shell sac pore finally comes to lie between the insertions of the posterior edges, along with the lateral branches of the anchor-shaped scar (See p. 205).

In ventral aspect the still-open funnel tube is visible, the anal papilla and the gills are not yet entirely retracted into the mantle cavity. Anterior to the anal papilla, a bulgy hump appears; it probably represents the rudiment of the roots of the Adductor
239 pallii medianus, which is so characteristic for the sepiolids; the insertion on the mantle is hidden from sight.

Stage XIII-XIV (Pl. 23, Fig. 5) is best compared with the same stage of *Sepia* (Pl. 16). The identification as *Sepietta oweniana* is not ascertained beyond doubt; an absolutely positive determination is not possible.

The arms still exhibit the outer longitudinal furrows, dividing each arm into a medial and a lateral part. It is noteworthy that in the third arm only the medial, in the second arm only the lateral, part continues into the sharply demarcated arm pillar. The head cover derived from the medial parts of the dorsolateral and dorsal arms are very thin at this stage, as is normal (Pls. 4 and 5), so they could easily be overlooked.

The posterior connecting piece (hb) of the corneal fold already forms a distinct ridge; in contrast to *Sepia* (Pl. 16) it is not situated on the border between two portions of the white body, but forms an independent element, not yet united with the ocular edge formed by the corresponding arm pillars.

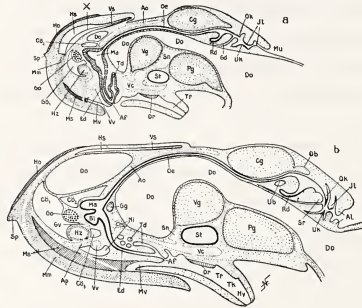
The funnel pouches are rather completely covered by the mantle rim, and the dark zone (medially interrupted by a light strip) between the anterior parts of the pouches (cf. Pl. 23, Figs. 5 and 6) indicates the position of a nuchal cartilage, which is never differentiated in the Sepiolineae, in contrast to the corresponding stages of *Rossia* and *Heteroteuthis*.

On the surface of the mantle rudiment, Hoyle's organ (ho_1 , ho_2) appears very clearly; its posterior edge still shows a tiny depression marking the scar of the shell sac pore. The fins are shifted further anteriorly, so that the shell pore now lies far
240 behind the line connecting their posterior rims. The fin insertion lines become shorter, thus preparing the differentiation of the rounded, nearly circular fins typical for sepiolids.

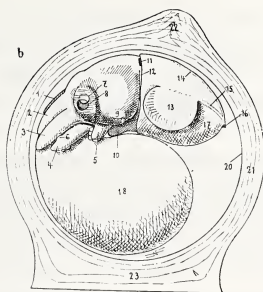
At stage XIV-XV (Pl. 23, Fig. 6; Textfig. 99) the arms have become longer. Their length relationships vary slightly from one species to the other; but the arm formula remains 3, 2, 4, 1. The arm tips are slightly pointed and continue to form new suckers; at the arm bases, knobs indicate the rudiments of buccal pillars (6 in Textfig. 99). The tentacles (4 *ibidem*) are subdivided into a stalk and a club. On the outside, the glandular lines (7) are now visible; they reach across the head covers. The ocular edges (9) of the latter are dorsally united with the posterior connecting piece of the corneal fold; on the ventral side, this connection is at least prepared, in that the posterior end of the edge is linked, by a delicate furrow (25) to the connecting piece, thus indicating the
241 remaining distance to be covered, similar to what has been observed in *Loligo* and *Sepia*. The integumentary part corresponding to the nuchal attachment (14) becomes more distinct, even in the Sepiolineae where an attachment is not formed.

At the posterior end, close to Hoyle's organ (17, 18) but isolated from it, a hard, pointed tubercle has formed; it corresponds to the soft terminal tip of *Sepia* and to a similarly situated hump on the mantle end of *Spirula*; the latter is formed only during postembryonic development, however (Vol. 1, p. 516). Here it will be termed the terminal spine. It is an embryonic organ like Hoyle's organ and might essentially serve the hatchling when perforating the egg envelopes (pp. 139, 109) which have been softened by the secretion of Hoyle's organ. It disappears within a few days after hatching. The fins now occupy the laterodorsal position typical for the family.

Further development, much as in *Sepia*, leads to definitive growth in length of the arms, differentiation of the tentacle clubs and of the buccal lappets, closure (somewhat accelerated) of the corneal fold, definitive formation of the head covers, delimitation of the olfactory tubercle and enlargement of the mantle pouch.



Textfigure 100. — Medial sections of two embryos of *Sepietta oweniana*. semi-schematic. (Stages XIV and XVII; from Vol. 1, p. 565; about 30× natural size). In a), note the large posterior part of the shell sac corresponding to the phragmocone (Hs: shell membrane drawn for illustration), on which the muscular mantle (Mm) inserts in typical fashion. In b), the shell sac has already retired from the posterior part, but the muscular mantle has not been able to follow; it remains in contact with it by an atypically structured membrane, which will subsequently be replaced by truly muscular tissue. Note the terminal spine (Sp) of the body and Hoyle's organ (Ho). As for the inner organs, the fixation of the gonad (Go) is of special interest: in a), it still has the typical embryonic form, whereas in b), the genital ligament, which connects the gonad to the posterior wall of the coelome (Cö), has grown very thin; it will subsequently be torn apart altogether (cf. Vol. 1, p. 486). The following organs are recognizable: mouth opening (Mu), the upper and lower beak (Ok, Uk), the subradular organ (Sr), the salivary gland duct (Gd), the radula pouch (Rd), upper and lower buccal ganglia (Ob, Ub), cerebral ganglion (Cg), pedal ganglion (Pg), "visceral" ganglia (Vg), statocyst (St, tangentially cut), foregut (Oe), stomach (Ma), caecum (Bl), hindgut (Ed), ink duct and gland (Td), Vena cava (Vc), Ganglion gastricum (Gg), kidney (Ni), pericardium (Cö), heart (Hz), gonad (Go), yolk organ (Do), mantle cavity septum (Ms), anus (Af), funnel organ (Dr), rudiment of funnel valve (Tk), funnel tube (Tr), the latter is closed by a membrane (Hy).

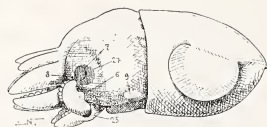


Textfigure 101. — Embryo of *Sepietta oweniana* in its envelopes, in natural position. 25× natural size (same as Textfig. 58, cf. Textfig. 102).

1-5: arm rudiments; 6: rudiment of swimming membrane of tentacular club; 7: pupil; 8: primary lid; 9: olfactory tubercle; 10: funnel tube; 11: nuchal attachment; 12: funnel pouch; 13: fin; 14: Hoyle's organ, medial branch; 15: lateral branch; 16: terminal spine; 17: mantle sac; 18: yolk sac; 20: chorion; 21: gelatinous envelope; 22: tip of the latter, apparently formed at the end of capsule extrusion; 23: base.

Note the marked shift of the fins compared to the rudimentary condition (Pl. 23, Fig. 2), the still typically decapodan structure of the nuchal area (11), the relation of the primary lid to the pupil, the position of the olfactory organ, and the arm proportions which are characteristic for the *Sepietta* group.

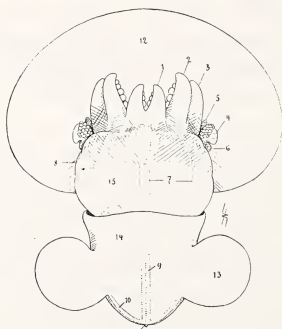
At stage XVII (Textfigs. 100 b, 101) these processes are considerably advanced. The embryo is situated in a natural attitude inside the envelopes; these envelopes are shown in optical section in Textfigure 101. As is typical for decapods having a large yolk mass, the embryo is bent against the yolk sac, sitting on it, as it were. The yolk sac itself is pear-shaped, apparently somewhat compressed by the embryo, and has a posterior indentation (cf. Textfig. 103). The tentacular club shows a striking feature: on the dorsally oriented outer edge, a roundish wart or lobule (6 in Textfigs. 102 and 103) appears as the rudiment of the swimming membrane. Thus the latter is strictly limited to a very small area of the club length, in contrast to all the other decapods, and this peculiarity is retained throughout embryonic life. Later on, this condition is entirely retained, or at least in its essential feature in that the swimming membrane is limited to the proximal part of the club, where it forms a roundish lobe (*Rossia megalptera*, *R. glaucopsis* etc; *Stoloteuthis*; cf. also *Heteroteuthis*: Vol. 1, pp. 576, 598), or else the typical condition is reestablished secondarily in that the swimming membrane lengthens to attain the length of the club.



Textfigure 102. — Embryo of *Sepietta oweniana*. $19\times$ natural size (from Vol. 1, p. 570). Stage XVII-XVIII. Compare with Textfigure 101 to assess the transformation of the primary lid into a cornea. The edge of the primary lid has become a minute, anteriorly situated pore (8), while the circular zone behind (24) has become fully transparent, so that the pupil (7) can be seen even in a preserved specimen. Note also the sepioid curvature of the tentacular club with its characteristic rudiment of a swimming membrane (6). The shallow invagination at the base of the tentacular stalk is limited by the web (25) connecting the third and fourth arm. 9: olfactory tubercle.

The fin is differentiated (cf. Textfig. 102) by the enlargement of the anterior rim, which forms a typical “lobe of the ear”, and by the delimitation of a thin, marginal zone from the more massive, opaque “main plate”.

The contraction of the corneal fold is not achieved in a continuous process, as is the case in other forms, but each stage is variable in physiological terms (p. 117). But compared to *Sepia* (Pl. 19), the process is somewhat faster and occurs earlier in relation to the overall maturity of the embryo. Textfigure 102 presents it complete. At this stage, which can be considered to represent XVIII, the primary lid aperture is reduced



Textfigure 103. — Embryo of *Sepietta oweniana*, seen from above, complete with yolk sac. Stage XVIII. cf. Textfigure 102. $19\times$ natural size. — Note the beginning web formation between the arms. Drawn after preserved specimen; the yolk sac (12) is slightly expanded.

1-5: arms; 6: rudiment of swimming membrane on tentacular club; 7: glandular lines; 8: cornea; 9, 10: Hoyle's organ; 11: terminal spine; 13: fin.

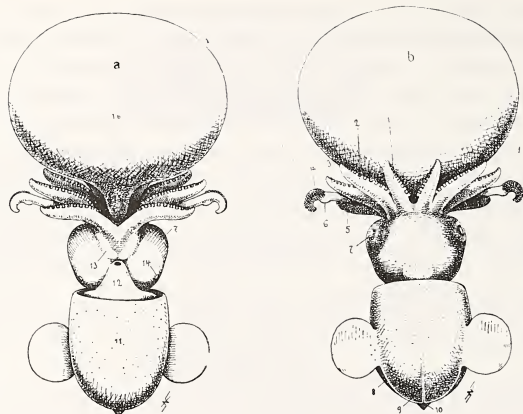
to a tiny pore, which will be closed completely in certain cases (*Heteroteuthis*), but which generally remains distinct. Behind it, above the iris opening, a roughly circular area, a sort of window, is visible as part of the corneal skin derived from the primary lid; this is the actual cornea, which is perfectly transparent, whereas the parts surrounding it are slightly opaque. It is surrounded by circular muscles, which will soon contract to produce a further skin fold, the so-called secondary lid.

Here we have to note a distinct deviation from the mode observed in *Sepia* (Pl. 19, Fig. 6) where the secondary lid appears before the delimitation of the definitive cornea, in fact even before the complete closure of the primary lid, so that a stage like Textfigure 102 does not obtain. An even more marked difference is that the secondary lid of sepiids includes the primary lid pore, whereas in sepiolids it excludes the pore (vol. 1, pp. 527 and 564). I therefore reject the idea that these two forms of lid are strictly homologous. I would rather call them homogenetic, assuming that they are derived from a common original condition in the ancestor (p. 255).

This assumption is suggested especially by *Idiosepius* (Textfig. 87), in which a third variant appears to obtain: when the muscles are completely relaxed, a secondary lid apparently is lacking altogether. Under moderate contraction, which always occurs when living specimens are placed in a fixative, the transparent cornea is surrounded by a distinct circular ridge, which forms a sort of frame. Inside it the delicate folds converge on a point close to the anterior border of the cornea (but still inside it), which is slightly elevated like a papilla. Here one would have to look for the pore of the former primary lid, in other words this pore would lie within the zone of the cornea proper; this would be even more different from the sepiolid condition than the sepiid mode.

244 Assuming for the three families a common ancestral condition similar to the picture given in Textfigure 102 (with the difference that the orbital pore would have to lie exactly at the anterior border of the corneal zone), formation of the three observed variants can easily be imagined, namely by unequal delimitation of the cornea against the surrounding, opaque and permanently more contractile parts of the primary lid. The resulting secondary lids would not be strictly homologous, however, although they could be considered to be derived from a common original condition. See also Vol. 1, pp. 488, 505 and 518.

At this stage, the terminal spine reaches the culmination point of its development, which is nevertheless a modest state compared to the condition of some species of *Rossia* (Textfig. 107).



Textfigure 104. — Embryo of *Rossia macrosoma*, virtually complete in its overall development, probably viable without the large yolk sac (16). Stage XIX. Naples, June 1st, 1912. — 9× natural size.

This embryo shows the typical overall aspect of an advanced sepiolid embryo, without any secondary modifications (cf. Textfig. 105).

1-5: arms; 6: rudiment of swimming membrane on tentacular club; 7: cornea; 8: lateral branch of Hoyle's organ; 9: medial branch; 10: terminal spine; 11: mantle sac; 12: funnel tube; 13: tentacular base inside the tubular tentacle pouch; 14: olfactory organ.

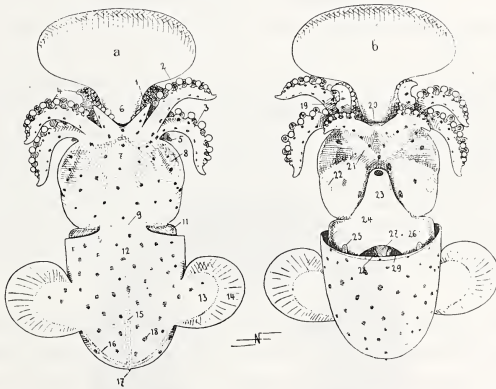
Stage XIX (Pl. 23, Fig. 9, Textfig. 104), a typical little *Sepiolo*, but still having a large outer yolk sac, shows no new surface differentiations, but a general approximation to mature conditions: the arms have grown strongly in length, the tentacular club shows the typical juvenile form (Textfigs. 105, 109). The roots of the tentacular stalks lie deeper and make contact medially with one another behind the ventral arms. Thus the typical tentacular pouches are formed, but only part of the actively shortened stalks can be retracted into them (in contrast to the situation shown in Pls. 18 and 19). The arm bases are connected by delicate membranes, except the ventral arms; the suckers are fully differentiated and their stalks sit on peculiar cushions which raise the suckers above the arm surface.

The eyes are very large and are shifted laterally on the head at varying stages, depending on the species, sometimes (Textfig. 109) only during postembryonic stages; the olfactory tubercles become notably smaller. At the base of the funnel tube, between the tube and the funnel pouches, the lateral funnel adductors are now visible

as delicate skin muscles that reach to the head; on the funnel corners the first small rudiments of the elongate funnel attachments are distinct.

The mantle sac is strongly expanded and now has the typical pouch form. The difference from mature conditions lies essentially in the presence of embryonic organs: 246 the yolk sac, Hoyle's organ, and the terminal spine. The mantle cavity shows the typical features of the family.

Whereas up to here, rather typical sepiolid features were mentioned for the observed Sepiolinae, we now have to turn to a formation that is typical for the subfamily, namely the nuchal band. It is fully developed at stage XIX, although it is often so highly transparent that one might believe he sees a free dorsal mantle rim. This band is nothing other than a fusion of the mantle and head skin in the area where a typical nuchal attachment would form. This organ begins to show as a rudiment, at earlier stages, much as in *Sepia* or *Rossia* where it also is a final differentiation of the

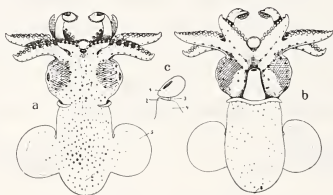


Textfigure 105. — Embryo of *Sepietta oweniana*, 19× natural size. Stage XIX. Note the generalised sepiolid type in comparison to Textfigure 104. Characteristic features of the subfamily Sepiolinae are the nuchal band (9) between the head and the dorsal mantle rim, and the relatively sparse chromatophores. The subgroup of the *Sepietta*-like forms is recognizable by the particularly weak development of the dorsal arms and by the shape of the yolk sac.

1-5: arms; 6: yolk sac; 7: buccal mass, visible through the integument; 8: eyes; 9: nuchal band; 11: funnel pouch; 12: mantle sac; 13: main plate of fin; 14: membranous rim of fin; 15, 16: Hoyle's organ; 17: terminal spine; 18: chromatophore; 19: rudiment of swimming membrane on tentacular club; 20: buccal pillar; 21: base of tentacle, visible through the integument; 22: olfactory organ; 23: funnel tube; 24: lateral funnel adductor; 25: mantle attachment; 26: funnel pouch; 27: hindgut; 28: root of Adductor pallii medianus; 29: funnel rim.

dorsal side (Textfig. 99 b; for comparison see Pl. 16, Fig. 6). A sharp delimitation is not achieved, however, and at stages XVII and XVIII the dorsal mantle fold becomes connected to the head while the rather shallow cavity of the underlying mantle disappears. At stage XVIII-XIX this connection reaches the outer surface, so that the conditions for the development of a direct skin bridge between the head and the mantle rim, as shown in Textfigure 106, is achieved.

The formation of the actual nuchal band thus is prepared by the degeneration of the dorsal mantle slit (Textfig. 100); in the Sepiolinae this slit never penetrates deeply



Textfigure 106. — Nearly mature embryo of *Sepiola robusta* or *ligulata*. Stage XX. From Volume 1, page 606, $6\times$ natural size (cf. below, p. 249). — Characteristic features of this species are the size, the strong, fleshy structure, the reddish brown coloration and the distribution of the dark chromatophores (the yellow ones are faded out), and also the broadly rounded fins (cf. Textfig. 105). Note also the differentiation of the suckers (inset) which differs from that of adult suckers, the typical shape of the sucker carriers (4) with the distinct rudiment (2) of a swimming membrane support, the relic of a terminal spine (8) and Hoyle's organ (6, dotted lines), the distinction of the membranous fin margin (5), the typical mantle rim (slightly retracted due to fixation), the glandular lines on the head (7), the contracted, pouch-like lid which is open dorsally, the still virtually embryonic condition of the olfactory tubercle. The animal is only slightly deformed due to fixation; but the mantle is very strongly contracted, so that the head appears unnaturally large. See Textfigures 104 and 108 b for a more normal sepiolid shape!

247 into the mantle, and between stages XV and XVIII it progressively disappears in the anterior direction. When observed closely, this process is not really a fusion (a term I have used in a somewhat figurative manner); it is the regression of a degenerating rudiment. Only after the disappearance of the dorsal mantle slit (Textfigs. 102, 103) does the skin connection between head and mantle form.

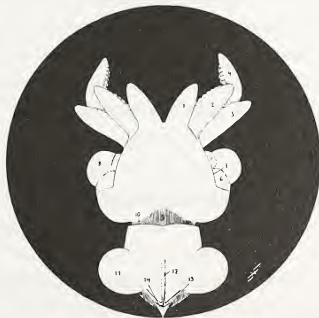
By stage XVIII, the sepiolid features are established, and with the nuchal band rudiment the typical aspect of the Sepiolinae is achieved. Textfigure 105 shows this aspect more eloquently than words. When artificially deprived of its yolk sac, such an embryo can continue to develop in a small aquarium with sandy bottom; it thus offers a perfect object for physiological and ecological observations. The chromatophores,

which first appear during stages XVII and XVIII, rapidly attain the species-specific arrangement and density. Normally the resorption of a yolk sac like that shown in Textfigure 105 takes about 7 days.

3. On the Embryonic Development of *Rossia*

Unfortunately only a few poorly preserved embryos of *Rossia* were available, and on two occasions I got only one single living egg. The first of these provided the same picture as stage I-II of *Sepia* (Plate 13, Figure 6), although the germinal disk was much smaller, less than 1 mm in diameter excluding the plasmatic rays. The whole egg measured 5 × 6 mm. The second egg contained the embryo shown in Textfigure 104. Eggs with their envelopes are figured by Jatta (1896, Plate 8, Figure 4).

To fill at least part of the gap, I will consider a rather young embryo of *Rossia glaucopsis* from Bergen (Textfig. 107). This is a stage corresponding to Textfigure 99 and Figure 6 of Plate 23, so that special explanations are not necessary. Only a few proportions are peculiar: the arms are very long already, and the head covers are more developed than in the corresponding Sepiolinae. The same is true with regard to the nuchal area (9 in Textfig. 107), which has to be considered the anlage of the nuchal



Textfigure 107. — Embryo of *Rossia glaucopsis*, from Bergen. 13.5× natural size. On top of the globular yolk sac (drawn in black), the embryo lies in typical position. Note the very strong development of the arms and tentacles (1-4), head covers, nuchal disc (9), terminal spine (14) and compare with Textfigure 99 b.

attachment. Especially well developed is the terminal spine (14), which is also very conspicuous in the embryo of Textfigure 104; we can thus assume that this strong development represents a typical feature of the genus *Rossia*. Since *Rossia* clearly shows the archetypal form of the family, the terminal spine will have to be considered as an organ undergoing regression rather than as a rather new acquisition.

From a notice by Froriep (1850, p. 192) it can be seen that Steenstrup already observed this formation in *Rossia oweni* as a shield-like, almost horny plate with a spine in the center. Around the latter he observed concentric stripes. Apparently the terminal spine is particularly strong in this species.

248 The embryo of *Rossia macrosoma* shown in Textfigure 104 is an almost complete young animal. But the very large yolk sac indicates that it is far from having reached its definitive size; the hatchling is probably more than twice as big. The arms show 4 rows of sucker rudiments, two at the proximal end. The arm length formula is 3 2 4 1, and the arm bases are connected by small velar membranes. The tentacular stalks are already fairly long, their roots being hidden in deep pouches. The clubs carry 8 rows of small suckers on the broadest part; the typical embryonic swimming membrane is limited to the basal part. This is a striking feature, since the juvenile animal, perhaps even the prehatching embryo, shows the normal sepioid condition of the tentacular club (cf. Textfig. 92 and p. 233, along with Vol. 1, p. 593); so this peculiar feature, viewed in a phylogenetic perspective, appears as a regression (page 253).

The head exhibits fully developed eyes, except for the secondary lid, but they are still oriented anteriorly; the olfactory tubercles on the "cheeks" (14 in textfig. 104) are now strikingly small. The mantle pouch shows the typical shape, as do the outline of the fins and Hoyle's organ. The size of the terminal spine is considerable when compared to Textfigures 99-101, which show the condition in Sepiolinae.

4. On the Embryonic Development of the Genus *Sepiolo*

249 The eggs of the different species of *Sepiolo* are not distinguishable with certainty. Among the eggs collected in the bay of Naples and adjacent zones, those showing a distinctly yellow brownish color (like the eggs figured by Jatta, 1896, Pl. 7, Fig. 7 and Pl. 8, Fig. 2) regularly contained embryos of *Sepiolo*, whereas the greyish white

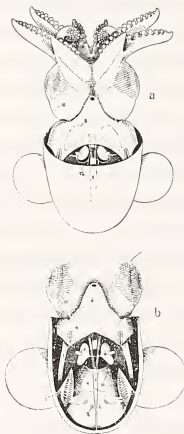
ones (Vol. I, Pl. 19, Figs. 15 and 18) mostly contained embryos of the *Sepietta* group. This rule has not remained without exceptions, so it can be used only in support of other characters (pp. 262-266), especially for material collected close to the coast and in the vicinity of the Zoological Station.

In contrast, the above rule was fully confirmed with material collected from the "Ammontatura" (outside of Nisida) and from the "Secca di Benta Palummo" (outside of Capo Miseno). These zones are elevations of the sea bottom that are continuations of coastal elevations; several cephalopod species appear to spawn preferentially there. Among them *Sepietta oweniana*, *Rondeletiola minor* and one or several species of *Sepiolo* are of interest here. *Sepiolo* spp. lay their light yellow brownish eggs on sponges, corals, worm tubes and stones; these eggs are of considerable size (p. 71), develop readily in an aquarium and finally release young animals of brown reddish color, which are the largest, strongest young *Sepiolinae* ever observed in this area.

I now suppose, given the size of the oviducal eggs in this species, that they belong to *Sepiolo robusta*, despite the fact that in the same locations most of the adults caught are *Sepiolo ligulata*, so that the latter cannot be definitely excluded from consideration. The embryos taken from this material were considered to be *Sepiolo ligulata* when Plate 23 was prepared, as were (with a caveat) the young animals hatched from these eggs (Vol. 1, p. 606). What argues in favor of *Sepiolo robusta* are the particular size (the eggs measure 3.6×4 mm) and the color of the hatchlings, although the color might be a more generalized juvenile condition.

At the same sampling station, eggs of *Sepietta oweniana* can be obtained almost year round; these embryos are distinguishable from *Sepiolo* embryos by the more strongly developed dorsal arms (Pl. 23), stouter, bulkier body, relatively short mantle (cf. Textfig. 99); but a really major significance of these differences should not be claimed since identified comparative material is not yet available. Overall this material corresponds to the above description (pp. 246 to 259), but a closer look at the ink sac area is now necessary: in this area, at stage XVII, one finds epithelial thickenings on either side of the slightly broadened ink sac; these thickenings are similar to the rudiments of accessory nidamental glands (Textfig. 56), from which the luminous glands are formed later. As discussed in Volume 1 (p. 582), these luminous glands are typical, in systematic-morphological terms, for the whole group of the *Eusepiolinae*, but since they are strongly modified or suppressed in the *Sepietta* group, they will be described here.

250 The typical luminous glands of Sepiolineae are formed during embryonic development, and in the species considered here they attain a condition that is representative for the typical, unmodified (*Sepiolo*-like) Sepiolineae, in other words, for the whole subfamily excluding *Sepiolina*.



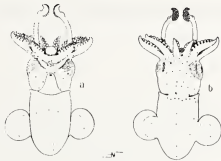
Textfigure 108. — Advanced embryonic stage (a) and newly hatched animal (b) of *Sepiolo robusta* or *ligulata* (a: 12/1, b: 8/1).

Note the formation of the luminous glands (6) associated with the laterally drawn out ink sac (12). In a), but also in much younger embryos, it is oval in outline, the papilla with the pores (5) is elongate; in b) it is already ear-shaped, connected to its counterpart by a muscular strand. This characteristic organ can be easily recognized in advanced embryos of *Sepiolo* (i.e. it is distinguishable from the similar organs in the *Rondeletiolae* and *Sepiidae*). — a) shows furthermore: mantle sac and fins, funnel pouches and funnel tube, funnel gland (8) and funnel attachments, and the still frail lateral funnel adductors. In the mantle cavity, the branching Adductor pallii medianus (1) is visible, next to it the *Nervi viscerales*, the anal papilla; in the head, one recognizes the eyes, the olfactory tubercles (10), the tentacular base (visible through the integument), the arms with the characteristically shaped suckers and sucker carriers, the tentacular clubs, the web rudiments, the buccal funnel. — b) shows: the enlargement of the funnel gland, a shifted position of the eyes and olfactory tubercles. In the mantle cavity note: funnel retractors (7), gills, branchial bands (still short), branchial spleen (3; shining through the surface), kidney papillae. Note especially (between the branchial hearts) the rudiments of the nidamental glands (2) and, more anteriorly, behind the kidney papillae (14), the epithelial zone (not yet distinct) from which the accessory nidamental glands (4) will be formed later. — In a), the yolk sac is removed; its is much larger than the head.

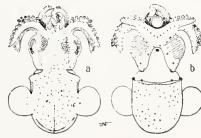
At early stages (XVII) they form opaque patches on either side of the superficially located, broadened ink sac; sections reveal their structure, which is characterized by

epithelial proliferation with rudiments of invaginating glandular tubuli. Later (Pl. 23, Fig. 3, Textfig. 108a), one observes oval, translucent (opaque, whitish after fixation) bodies embedded in lateral pouches of the ink sac. The outlets of the glandular tubuli are united on a prominent papilla on each side of the organ. Medially the two glands are totally separated: between them lies the intestine, flanked by the two roots of the Adductor pallii medianus.

At the most advanced embryonic stages (Textfig. 108b) the organ has a more bean-shaped aspect; the papilla of the glandular outlets is less prominent, so that the organ is now rather similar to the definitive aspect. In the Mediterranean (i.e. *Sepiola*-like) *Sepiolineae*, a typical feature is the double row of sucker rudiments on each arm; this represents the reestablishment of an older (more general) norm than that of the *Sepioidea*.



Textfigures 109.



Textfigure 110.

Mature embryos of two different species of *Sepiola*. From Volume 1, page 608.

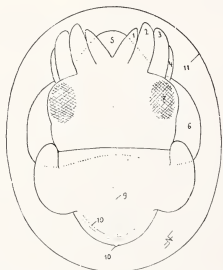
Textfigure 109 possibly represents *S. steenstrupiana* or *aurantiaca*; Textfigure 110 *S. affinis* or *rondeleti*.

Other *Sepiola* embryos. Occasionally and generally by mere chance, single eggs of *Sepiola* were found on stones, corals, bryozoans, hydroids and algae; generally their identification to species is impossible. The small numbers did not permit complete description of their development; as far as the younger stages are concerned, no great differences were observed. Suffice it to figure two forms of embryos obtained from such eggs. They clearly do not belong to any of the above-described species, and they are quite different from one another. The mature embryo shown in Textfigure 109 is noteworthy for its slender shape of the body, the still small size of the eyes which are oriented anteriorly (cf. Textfig. 68), features that are strangely atypical, indicating that the species of *Sepiola*, which I now distinguish, are by far not as closely related as one might believe considering how mixed up and confused they were up to now.

5. On the Embryonic Development of the Genus *Sepietta*

The eggs of *S. oweniana* (Vol. 1, Pl. 19) are regularly collected together with eggs of *Sepiolo robusta* (*ligulata*?) at the sampling stations of the Ammontatura and Secca di Benta Palummo (Page 261). They are distinguishable from the latter by their small size and light color (or lack of coloration) of the gelatinous envelopes. The older embryos also can be distinguished easily from eggs of the genus *Sepiolo* by the lack of luminous glands; in fresh specimens the ink sac is recognizable across the mantle tissue and shows a simple pear-shaped outline without lateral expansions. If one gets a batch containing 10-20 eggs, one can raise the stages and be certain of the identification at the end of the culture.

The eggs are not definitely distinguishable from those of *Sepiolo* species producing small eggs (See Textfigs. 109, 110 and 112). They measure 2×2.4 mm. Some of the embryos figured in Plate 23 clearly belong to *Sepietta oweniana*, as do the specimens shown in Textfigures 99, 100, 101, 102, 103, 111 and 112. Textfigure 111 is drawn after a living embryo from amongst eggs that were raised to hatching. Compare this sketch with Textfigure 103 and note the natural posture of the animal, and especially the characteristic form of the yolk sac, which is directly visible or shining through the embryo.



Textfigure 111. — Embryo of *Sepietta oweniana* inside its slightly expanded chorion [11]. Stage XVII-XVIII. $19\times$ natural size. Drawn from life. Note the characteristic position of the embryo in relation to the yolk sac, and the shape of the latter; for explanation see Textfigure 103.

At stage XIX the embryo provides the picture given in Textfigure 105. Compared to embryos of *Sepiolo robusta* at comparable or earlier stages, it is smaller and more delicate, has the eyes in more markedly anterior orientation, and chromatophores in much looser distribution. The fins have a very broad rim of thin tissue. The yolk sac is still drawn out laterally, with a basal part forming a stalk.

The arms are clearly unequal from early stages onward, very markedly so at later stages, the dorsal and ventral arms being much shorter than the lateral arms. The fully developed young animal is shown in Textfigure 112.

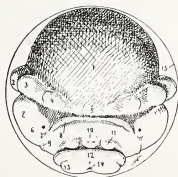


Textfigure 112. — Newly-hatched *Sepietta oweniana*. $6\times$ natural size. From Volume 1, page 648. This figure illustrates the typical features of the Sepioliinae better than Textfigures 106 and 110, because the specimen shown here was more carefully narcotized and preserved.

Other *Sepietta* embryos. From inshore waters of shallow depth, eggs of *Sepietta* have also been collected; they are somewhat smaller and more delicate than those described above and presumably belong to *Sepietta obscura*. The eggs of *S. obscura* measure 1.9×2.2 mm. Apart from these, I have not found any other peculiar features in these embryos, which otherwise are very similar to *S. oweniana*.

6. On the Embryonic Development of the Genus *Rondeletiola*

Close to the above-mentioned sampling stations (p. 261), but partly from greater depths (200 m), some eggs occasionally have been collected that are distinguishable from eggs of *Sepietta oweniana* by their very small size (cf. Vol. 1, Pl. 19). They measure on 1.3×1.5 mm and are thus distinctly marked for their difference. Their development is notably different from the typical mode of other Sepioliinae, although some traits are particularly similar to the development of *Sepietta oweniana*. There can be no doubt that they belong to the *Sepietta* group, and within the latter they can only belong to *Rondeletiola*, which is the form with that egg size. It thus appears that this

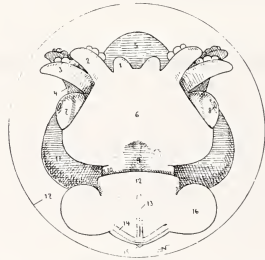


Textfigure 113. — Embryo of *Rondeletiola minor* inside its chorion (15). Outline drawn from life. Stage X. $25\times$ natural size. Note the peculiarly small yolk sac (1) and the still rudimentary ventral arms showing the bipartite initial condition (4).

3: tentacular arms; 2: third arm pair; 5: medial rudiment of arm crown; 6: stato-cyst (open pore); 7: ocular area; 8: funnel tube rudiment; 9: funnel pouch rudiment; 10: anal papilla; 11: gill rudiment; 12: muscular mantle; 13: fin; 14: shell sac pore.

peculiar form occasionally comes to spawn at lesser depths than where it normally lives (Vol. 1, p. 639).

The germinal disk resembles that of *Alloteuthis*, as far as its relation to the yolk mass is concerned, and thus differs from all the sepiolid relatives. The peculiarity (p. 176) is that the embryo cap is relatively large and thus encloses a much greater part of the yolk than is the rule in related species, although among the latter there is again some variation in this respect. At stage X (Textfig. 113), the yolk sac of *Rondeletiola* represents less than one half of the whole, so that also a certain similarity to the developmental mode of oegopsids may be seen here. The arm rudiments are strikingly unequal, the ventral ones strongly retarded, the dorsal ones barely visible.



Textfigure 114. — Embryo of *Rondeletiola minor* within slightly expanded chorion, in natural position. Fins artificially flattened. State XV; 27× natural size. This figure should be compared with Textfigures 99, 107 and with Plate 23, Figure 6. Note the inhibition of the dorsal arms (1) and the peculiar shape of the yolk sac (5). For further explanations see Textfigure 99.

254 As is typical for most cephalopod embryos, the embryonic body continues to contract and thus becomes partly retracted from the yolk mass; a considerable part of the yolk enclosed at stage X is indeed pushed into the outer yolk sac. The latter nonetheless remains rather small, although it later on shows a shape (Textfig. 114) that is typical for the *Sepietta* group among the Sepiolinae. The unusual relative sizes of the arms are also partly retained so that the species might be recognized from later
255 embryonic stages. The ventral arms indeed remain stubby, the dorsal ones completely rudimentary, whereas the other arms grow very strong. The disparity becomes less marked towards the end of embryonic development, but is still very distinct in the hatchling (Vol. 1, p. 631). At that stage, the paired rudiments of the luminous glands



Textfigure 115. — Juvenile form of a typical, *Sepietta*-like sepiolid (*Rondeletiola* or *Sepietta*); from Volume 1, page 631; 6× natural size.

The dorsal view shows nothing different from other *Sepiolo*-like Eusepiolinae (Vol. 1, p. 584). In contrast, the mantle cavity reveals a remarkable recessive development of the accessory nidamental glands (1); if this specimen represents *Rondeletiola*, these rudiments also include the modified luminous glands (Vol. 1, p. 632). Here the organs are united instead of being separately (in time and space) derived from rudiments as shown in Textfigure 108 (4, 5, which is typical for our Eusepiolinae); this union can be explained in either one of two ways only: either this is the archetypal condition of all Eusepiolinae and Heteroteuthinae, which has been subsequently modified by temporal and spatial separation of the respective rudiments of luminous and accessory nidamental glands in the Sepiolinae so far observed, or this union reflects the suppression of a primary condition of this group (but secondary in the frame of the whole family), by omission of the ontogenetic factors responsible for its expression. At any rate, the zone lying between the kidney papillae, i.e. the archetypal position, in which the organ complex develop, is strongly shortened (as in *Rossia*: Vol. 1, p. 590), as can be recognized from a comparison with Textfigure 108. An original connection between the luminous glands and the accessory nidamental glands also is demonstrated by the persistence of positionally intermediary glandular parts in *Heteroteuthis* (cf. Vol. 1, p. 598).

become visible as opaque little patches on the lateral parts of the slightly broadened ink sac (cf. Vol. 1, loc. cit.).

These rudiments are also the rudiments of the accessory nidamental glands and thus confirm my theory according to which the luminous glands are derived from the accessory glands, since they again can be united in the rudimentary state (cf. Vol. 1, pp. 574-575, 635). The very interesting relationships that are thus suggested provide a new indication for the idea that a regression of morphological differentiation can uncover very old ancestral conditions that lie dormant in the conservative rudiments, often hidden by secondary influences (cf. p. 15).

CHAPTER 11

The Embryonic Development of the Octopods

The eggs of octopods are devoid of secondary, gelatinous envelopes, since nidamental glands are lacking in these animals. The secretions of the rather small oviducal glands are sufficient, however, to glue the tough chorionic capsules containing the eggs to one another or to the substratum carrying them. In contrast to the decapod chorion, the elongate chorion of octopods has a stalk-like extension at one end; the vegetal pole of the egg lies close to the stalk base (Textfig. 19). The eggs proper are generally much more elongate than is the case in decapods, often appearing almost cylindrical or sausage-shaped. (For the preparatory developmental processes see p. 277).

The cleavage was so far unknown. I have been able to observe it in *Octopus vulgaris* (for a detailed description see below, page 278). Cleavage ends with a single-layered blastodisc, which has a different aspect in *Octopus* (Pl. 24) compared to *Argonauta* (Pl. 32). It repeatedly shows central gaps (Pls. 24 and 32), but in no case the characteristic structure of the decapodan blastoderm (Pls. 1 and 13). The multi-layered ring, which is subsequently formed by cell shifting and submersion (Textfig. 31), is in a marginal position virtually from the beginning, because the few yolk cells are rapidly covered, the ring becoming inwardly broader.

256 Once the lower germinal layer, the endomesoderm, has reached the center (Pl. 25), here also a differentiation into prospective embryo body and yolk envelope is achieved belatedly; each of these components further on shows features similar to the

decapods: in the anlage of the embryo proper, mesoderm patches form, essentially as in decapods but less distinctly (Pl. 25). The subsequent folding produces an embryo in which the typical bauplan is recognizable.

However, only 4 arm rudiments appear on either side, in such a regular distribution that no traces of a suppressed rudiment can be seen. Thus one cannot observe directly which one of the decapodan rudiments is lacking, but simple observation of decapod embryos suggests that it is the dorsal arm pair. Definitely it must be one of the three dorsal arm pairs of decapods, and by no means the tentacle pair (See Pl. 4, Fig. 7 in comparison with Pl. 33, Fig. 11!).

The whole anlage of the embryonic body appears more blurred than in decapods (despite identical treatment), so that e.g. the statocyst rudiment is barely distinguishable as a diffuse, shallow depression.

The mantle rudiment provides a remarkable picture (Pl. 25, Fig. 6): the scanty shell sac is contracted very early, and on either side of its remaining pore, one can see the distinct but poorly developed fin rudiments (Pl. 37). Only *Argonauta* (Pl. 33) does not show them at all. The muscular mantle develops in inverse relation. It increases in size in reversed proportion with the receding shell (Vol. 1, p. 657); this is a general developmental trend in dibranchiates, but here it is further enhanced.

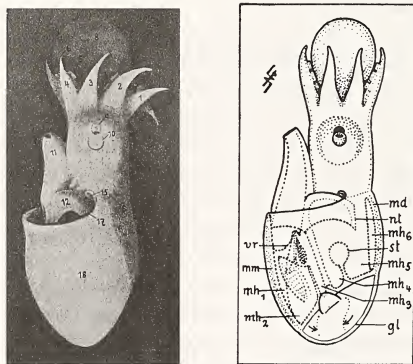
At early stages, the center of the mantle rudiment (Pl. 25, Fig. 4; Pl. 33, Fig. 4; Textfig. 129) is always occupied by a roughly circular, slightly concave epithelial plate, which can be identified, based on comparison with Plate 15, as the shell epithelium. This formation is generally very small and indistinct; I found it most distinct in *Ocythoë*. Appellöf (1899) therefore was unable to clearly recognize it and to follow its development, which provided support for the ideas of G. Steinmann*. However, it is not at all lacking in *Argonauta* and has the normal fate (Cf. Chapter 13).

In phylogenetic interpretation, the circular shell rudiment in the center of the muscular mantle of octopods (Pl. 33, Fig. 4) hints at an ancestral state that can be imagined in a way suggested by Textfigure 116b; in any case this is the type from which all the shell conditions observed in this order can be easily derived. However, its detailed development is not as simple as one might expect:

The replacement of the shell by the younger organ (i.e. the muscular mantle) does not take place the same way as it must have happened in phylogeny. The latter process

* Scientific Editor: Steinmann thought that octopods were naked ammonoids, an idea that unfortunately has come up again recently.

257 can only be imagined the way suggested by Textfigures 22 and 43, the shell sac and shell rim having been pushed backwards stepwise by the muscular mantle. Since the embryonic formation of a solid shell is postponed, this process could be easily "recapitulated" during ontogenesis in that the centripetally advancing muscular mantle (Pl. 33, Fig. 4) would slowly compress the shell sac rudiment. During such a process, i.e. in its different phases, one would then see variably ancient rudimentary states, exactly like those from which the different transitional forms of the ancestral series have been generated ontogenetically.



Textfigure 116. — Typical conditions in mature octopod embryos.

a) Mature embryo of *Octopus vulgaris*. 30× natural size. This form is far removed from the archetypal condition in that the fins are lacking, and the shell is strongly reduced in correlation with other secondary modifications in the mantle cavity.

1-4: arms of the left side; 5: sucker; 6: terminal flagellum; 7: web; 8: yolk sac; 9: pupil; 10: primary lid; 11: funnel tube; 12: funnel pouch; 13: entry to the mantle cavity; 14: entry to the funnel tube; 15: olfactory organ; 16: fusion between the head covers and the mantle rim (17); 18: mantle sac.

b) Ideal octopodan prototype at homologous stage, illustrating the particular conditions and permitting a comparison with the more general ones of Textfigure 55 (See this figure also for further explanations). The shell (gl) shows a condition that allows one to consider *Vampyroteuthis* and the primary stages in early octopod embryos as archetypal, indeed the only one permitting a derivation from a decapodan dibranchiate. The mantle cavity is correspondingly shallower (cf. positions of mh₃ and mh₂). The arrows indicate the secondary modification of the primary norm leading to the usual octopodan type; the shell is progressively "compressed" dorsally and ventrally by the parts of the muscular mantle (mm, md) corresponding to the posteriorly progressing ventral and dorsal mantle cavity, respectively. As a result, the shell turns into a roughly horse-shoe-shaped clasp supporting the posterior end. Note also the architecture of the mantle cavity: mh₁ is the ventral, paired cavity, surrounding the gill at mh₂; mh₃ dorsal to the branchial band, mh₄ dorsal to the insertion of the head-foot and funnel retractor; mh₅ lateral part, mh₆ dorsal to the insertion of the head-foot and funnel pouch, still separated from the ventral parts by the stellate ganglion (st) and the adjoining septum. vr: anterior end of the ventral septum of the mantle cavity; nt: seam between the muscular mantle and the mantle pouch.

However, as can be seen best in Textfigure 129 (as well as in Pl. 25, Fig. 6 and Pl. 33, Fig. 4), the shell sac rudiment of the known extant octopods (polypodoids) is much too small from the outset to establish the phylogenetically primary contact with the muscular mantle during early ontogenesis. The centripetally growing rudiment of the muscular mantle indeed encounters an empty space in the solid wall of the mantle sac; this gap no doubt corresponds to the *location* of a typical embryonic shell as it must be assumed for protodibranchiates (Textfig. 43), but it is by far not occupied by the shell sac rudiment, much less by a shell. The typical insertion on the latter can thus be established only later, once the progressively developing part has compensated the premature, as it were, regression of its antagonist.

A further detail has to be taken into account: the ectoderm and the adhering mesenchyme in the area of the above-mentioned gap (Textfig. 129, at 2) convey an impression, from the outset, as if they represented the outside of a closed shell sac. On it appear the fin rudiments, indeed within the muscular ring, and it is only after the central completion of the muscle ring that these rudiments establish an essentially normal relationship with the shell sac, i.e. take their position on its outside (Textfig. 129 d, at 5).

While the muscular mantle and the fins thus follow the more general scheme of dibranchiate development (Textfigs. 30, 36, 37) and indeed show a phylogenetically ancient picture, only rudiments of the shell parts conserved in extant polypodoids are formed, at first entirely detached from the parts that, in phylogenetical terms, are originally (typically) connected with them. So, not only is there no recapitulation of characters of conceivable adult ancestral forms, but embryonic features of very different age are combined in an architectonically and historically inconsistent way in the ontogenetic stages (See also Textfig. 129).

One might indeed consider this in contradiction to the law of conservative preliminary stages, viewing the ontogenetically primary insertion of the muscular mantle as a phylogenetically secondary state and the secondarily established insertion as an essentially primary state. However, such a view would overlook the fact that the young muscular mantle (in Pl. 25, e.g. Fig. 6) has *no insertion* at all, because its histological differentiation does not yet permit such a condition. What is available here is a cellular material that must be considered as amorphous with regard to a possible insertion (Cf. p. 22); but relating to its future role, it is also primary in phylogenetic terms as far as its position and coordination are concerned; it certainly shows no sign of a derived condition. It is on purpose that our law begins, in a qualified sense, with "*inasmuch...*"!

The peculiarities of octopod development becoming visible at later stages (IX-XX) can be summarised considering the different organs: the yolk sac exhibits differences in relative sizes similar to the decapods, and as in the latter these differences are related to the egg volume. But even in the forms producing very small eggs (Pls. 32 and 33), the formation of an outer yolk sac is not as much inhibited as in oegopsids (p. 180). In all instances the yolk sac lies in the body axis (Textfig. 116), rather than bent down ventrally as in decapods (Textfig. 58). This situation is related to the spatial conditions inside the chorion (Cf. p. 149) which do not require such a bending of the parts (Textfig. 123).

In the arm complex, there is no special differentiation of the rudiments corresponding to the decapod tentacles (compare Plate 21, Figs. 1-3 with Plate 28, Figs. 7-10). A careful comparison of development in the apical zone at later stages (Pls. 16 and 28) shows that the only two arm pairs present in octopods do not represent the three decapodan pairs in an equilibrated manner. Clearly, something is lacking in the zone of the first (dorsomedial) arm pair of decapods. This lack is obvious in the fact that the head parts normally covered by material derived from the first arm pair remain uncovered for a strikingly long time. Since in decapods (p. 168) the corresponding parts of the head cover are clearly more delicate than the rest (Pl. 23, Fig. 5; Pl. 4, Fig. 9), it seems inescapable to assume that the first (dorsomedial) arm pair of protodi-branchiates has been lost by the octopods; in all events the first and second arm pairs of octopods must be homologous to the second and third arm pairs of decapods, an assumption that is also supported by anatomical evidence.

One might remark, however, that the third arm pairs (i.e. the ocular edges of the pillars) undergo also some retardation during the formation of the primary lid (compare stage XV, Pl. 29, Figs. 1-3 with Plate 6, Fig. 6); but this retardation is of limited extent, in part only simulated by unequal conditions in the eye region. A comparison of stage XVI in Plate 6, Figure 7 (showing a fully covered buccal zone) and in Plates 29 (Fig. 6) and 35 (Fig. 1) is conclusive.

The sucker rudiments (Pl. 28) do not appear as continuous series on the arms; typically there are only three larval suckers in single file, whereas the free, whip-like arm tip remains bare for some time. The outer arm edges are proximally united by velar skin folds. The ventral surface of the head is also entirely clothed by the head
259 covers, except for the olfactory tubercles. The latter acquire a peculiar positional relationship with the mantle, which is characteristic for the octopods: in relation with the

formation of the nuchal fusion (See further below), each olfactory tubercle ends up at an extremity of the mantle slit (Pl. 29, Fig. 6; Pl. 30, Fig. 1); finally it is more or less completely hidden by the mantle rim. Sometimes it looks as if the mantle rim started directly from the dorsal side of the tubercle (Textfig. 116a), whereas in other cases, such a relationship is not visible. In general, the rather gelatinous constitution of the octopodan skin entails a lowering of the tubercle, so that a sort of olfactory pit appears. This very constitution of the skin hinders the resolution of the question whether such a pit is a typical morphological feature of the animal, i.e. an especially achieved condition, or a mere by-product.

260
261 The primary lid is formed following the general type. The posterior connecting piece is inconspicuous, similar to the teuthoid condition; it is easily overlooked (Pl. 29). A striking feature is the apparently greater area thus surrounded in comparison with decapods (Pl. 6). But it is of course more appropriate to say that here the enclosed parts of the ocular mass are comparatively greater in relation to the parts not enclosed.

In the mouth area, there is no trace of a buccal funnel (Pl. 28). There is also no nuchal attachment on the funnel complex. Such a formation is made impossible by a premature development similar to the condition in Sepiolinae (p. 257), which inhibits the formation of a mediodorsal mantle cavity (Pls. 27, 28). The rapid broadening of the nuchal fusion involving the head covers and the mantle rim also limits the funnel pouches on both sides (Pls. 29, 30).

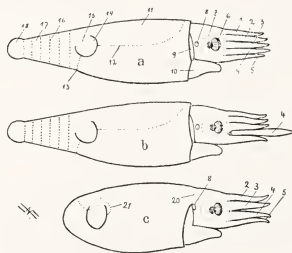
The fin rudiments disappear rather rapidly (Pl. 29, Fig. 6) in the polypodoid embryos (the only so far available for observation); it is not yet clear whether these formations are somehow related to the edges or seams of the skin that appear later in some species (they were termed lateral ridges in Vol. 1, pp. 675, 714). In the pelagic or abyssal cirroteuthoids, strangely specialised fins, in some rare instances lateral ridge-like formations, are developed (probably from similar rudiments).

The ventral, lateral and dorsolateral parts of the mantle cavity show some peculiarities (Textfig. 116 b): the mantle septum reaches far anteriorly (Pl. 29, Figs. 4 and 5: ms, ad) and forms the basis for the passage, to the mantle, of powerful muscle rudiments from the areas on either side of the intestine. They form an Adductor pallii medianus like in sepiolids. The gill rudiments are superficially similar to those of decapods, but early on they become attached on almost their whole length. The stellate ganglia (Textfig. 116 b) lie far apart (primary condition), and the more dorsally situated parts of the mantle cavity (excluding the mediodorsal parts!) extend

medially behind the nuchal connection, and furthermore extend anteriorly and posteriorly to form a peculiar secondary dorsal mantle cavity (mh_5 , mh_6), which is of paired origin (Cf. Vol. 1, p. 658). The paired origin of this space is due to the presence of a separating wall in the median plane, which soon breaks down, and the strong posterior extension (Textfig. 117; Pl. 37, Figs. 2 and 3) is primarily in an indirect relation with the ventral parts of the mantle cavity, whereas a secondary communication is achieved later behind the stellar ganglia and dorsally from the gills (Vol. 1, p. 664).

The typical aspect of a nearly mature octopodan embryo can be visualized by Textfigure 116, which allows one also to grasp relations with decapods. The latter are even better seen in Textfigure 117, but note that c does not represent the most generalized archetype of octopods, but a special case derived from Textfigure 116 b (See the small arrows there). Likewise b does not represent the most generalized archetype of decapods, but more specially a presepioid *sensu* Volume 1, page 791.

For the main variants of the octopod type, see Volume 1, pages 670-673. For all the Recent families, excepting the Vampyroteuthidae, a secondary compression of the shell zone in posterior direction is characteristic (Cf. Pl. 33, Textfig. 129), the shell thus being reduced to a horse shoe-like clasp bracing the body end. This clasp not only provides a support for the fins, but also for the insertion of the muscular mantle, in



Textfigure 117. — Schematic representation of juvenile forms: a) of an ideal protodibranchiate (cf. Textfigs. 28 and 30); b) of an ideal decapod; c) of an ideal octopod, in which the reduction of the shell to a horse-shoe-shaped clasp embracing the posterior end is achieved (for comparison see the more generalized type in Textfig. 116 b).

1-5: decapodan arms; 2-5: their homologs in octopods; 4: tentacular arm or its homolog; 6: primary lid; 7: eye ball; 8: olfactory organ; 9: funnel pouch; 10: funnel tube; 11: proostracum; 12: rim of the latter, where the muscular mantle inserts; 13: edge of phragmocone; 14: fin; 15: fin insertion line; 16: suture line; 17: gas chamber; 18: initial chamber; 20: seam between the cephalic integument and the muscular mantle; 21: shell.

which the shell rudiment is more or less completely embedded. In the archetypal octopod, which is most closely represented (in this respect) by the Vampyroteuthidae, the shell must have been a round, cup-shaped formation situated in the posterior part of the body roughly like a teuthoid cone (Textfig. 73). A proostracum is lacking in all instances; the dorsal parts of the muscular mantle occupy the area from early stages onward and cover the atypical dorsal mantle cavity. But note the feeble indication of a dorsal plate in Plate 37, Figure 8 and in Textfigure 129, represented by a dorsal indentation in the shell gap of the muscular mantle rudiment. See also Plate 33, Figures 4-10.

- 262 In the polypodoids, only the lateral parts of the restricted shell sac are conserved, whereas the medial connection is obliterated (See Textfig. 127 a, where it is still present at 7). In the argonautids, these lateral parts in turn degenerate, whereas they persist in the octopodids and accommodate the cartilaginous rodlets formed inside them as true shell remains (Appellöf, 1899).

CHAPTER 12

The Embryonic Development of the Octopodids

Contents: 1. Generalities. 2. *Octopus vulgaris* (p. 277). 3. Other *Octopus* species (p. 293). 4. *Eledone* (p. 294).

1. Generalities

Although the octopodids are among the most common and most intensively studied cephalopods, their embryonic development has so far become known only by small fragments; a comprehensive study apparently has never been done. The egg masses of these forms are also very rare in museum collections. Clearly, they show a very different aspect. Some species appear to spawn their large eggs one after the other (like sepioids) and to glue them to a solid body (rocks, shells) by means of the secretions from the oviducal gland (Vol. 1, p. 779), so that the eggs stand on their chorion stalks somewhat like club-shaped mushrooms; they are grouped in clusters (Cf. Vol. 1, p. 692) that supposedly are guarded somehow by the mother animal. Other species that also produce large eggs unite the chorion stalks to form small or sizable bunches, as is known with certainty from *Octopus punctatus* Gabb and from the genus *Eledone* (See further below). A third group producing much smaller eggs (p. 71), to which all the Mediterranean *Octopus* species belong, form long stems from the chorion stalks which are more or less strongly twisted; each egg thus has only a short free stalk and sits like a kernal (spicule) on an ear of corn (Cf. Jatta, 1896, Pl. 7, Fig. 2).

The course of development is probably not identical in the different eggs, and it seems rather likely that forms developed from large eggs would show the rudiments much more distinctly than is the case in the rather small eggs of *Octopus vulgaris*.
 263 Unfortunately it has not been possible in recent years to obtain eggs from a captive *Eledone* at Naples. (Mature specimens are indeed rarely caught.) No eggs have been collected from the field either. Our description must therefore deal essentially with the development of the most common form that spawns in the aquarium.

2. The Embryonic Development of *Octopus vulgaris*

Even this most common form was hitherto almost unknown as far as its embryology is concerned. A certain number of stages are figured by Korschelt & Heider (1893, Vol. 3), and a few special indications and figures are due to Appellöf (1899). But these elements are far from providing a comprehensive idea of the development of this interesting animal.

The following description is based on several large egg masses that were spawned in the big tanks of the public aquarium of the Zoological Station during the summer months (middle of May to end of August) of the years 1911-1913. These egg masses always developed poorly in my own care (in running water), whereas development was generally quite normal (up to hatching) when the eggs were left in the care of the mother animal. My experience in this matter has incidentally become known to Prof. Monticelli, who eagerly reported on it (1921). On the type of care, see Lo Bianco (1909) and Naef (1922, p. 292; 1923, p. 779). It is not yet clear whether the continuous water flow and the incessant (streaking and combing) movement of the egg strings due to action of the [mother's] arms are the only factors promoting development; they seem indispensable at any rate.

The eggs are strikingly elongate, almost sausage-shaped (Textfig. 19) and normally are positioned in the chorion capsule with the formative material lying at the side opposite to the stalk, in other words the animal (posterior) pole faces outwards. (About the consequences of an inverse position see Vol. 1, p. 687, and Fisher, 1925).—At laying the eggs are still immature and the formative cytoplasm is concentrated in a small spot. The first maturation division occurs immediately after laying, probably due

to the penetration of the spermatozoon during the passage through the distal oviduct; in eggs observed about 2 hours after spawning (the exact point in time is difficult to determine if one refrains from disturbing the long-awaited spawning event) I found the first polar body extruded (Pl. 24, Fig. 1); one hour thereafter, there were generally 3 polar bodies (Pl. 24, Fig. 2), the first one having divided again while a second one was extruded.—Afterwards the germinal disk expands (Fig. 3) thus preparing the onset of cleavage. The first cleavage furrow appears only about 9 hours after laying (Fig. 4). After 12 hours 4 cells were formed, after 15 hours 8 cells, after 19 hours 16 cells, after 23 hours 32 cells (at a water temperature of 23°C; these observations were made on July 4, 1913).

264 The 2-cell stage does not show any peculiarity, no more than the 4-cell stage (Fig. 5), in which sometimes (but by no means regularly) the posterior 2 blastomeres are distinctly smaller than the anterior ones, the transverse furrow being slightly bent to run in posterior direction from the center (Cf. Pl. 1). The orientation of the embryo is nevertheless possible in the normal configuration, since the polar bodies always mark the anterior part of the first furrow, as demonstrated by single eggs followed through the stages. However, the polar bodies lie rarely directly on the first furrow, but generally slightly shifted to the right or left side.

The third cleavage step already shows the deviation from decapods very distinctly (Fig. 6): 2 lateral on either side, and 2 anterior and posterior medial octomeres are formed. Normally the 4 medial octomeres are completely similar to one another and differ from the lateral ones (as in decapods) in that they come together at the transverse, second furrow, whereas the lateral octomeres are widely separate from the medial furrow. Figure 5 of Plate 24 shows that the third cleavage step does not start from the center, but from two points lying to the right and left of it. The difference from the decapods is given by the lower medial octomeres, which do not show the narrow, stripe-like shape typical for decapods (Pl. 1). However, atypical 8-cell stages do occur occasionally (Pl. 24, Fig. 7); they are indeed very reminiscent of the decapod condition. (The example figured is the most extreme deviation from the normal aspect!).—In all instances a broad gap forms from the central part of the transverse furrow which lies between the medial octomeres; this gap persists for a long time and closes only towards the end of cleavage; sometimes it even persists into the earliest stages of germ layer formation (Pl. 24, Fig. 17).

At the fourth cleavage step, essentially the same process occurs as in decapods: the 4 lateral octants divide radially, the 4 medial ones centrifugally so that 4

micromeres are generated along with 12 macromeres. The ligation of the micromeres is due to a slanting furrow (the medial end being more or less distinctly oriented towards the periphery) rather than by a simple transverse furrow; interestingly the upper and lower octants show exactly the same pattern, whereas in decapods the lower octants give off micromeres by simple transverse cleaving. The upper and lower sides of the germinal disk continue to be symmetrical to the transverse furrow even during the subsequent stages. A relatively frequent aberrancy is the occurrence of incomplete micromeres derived from the upper medial octants; as we have already seen in *Sepia officinalis* (Pl. 13, Fig. 3), the inner end in each of these cells looks like a micromere, whereas the outer end remains in continuity with the yolk (Pl. 24, Fig. 9). However, this aberrancy in octopods seems to be corrected subsequently, whereas it continues to show its effect in *S. officinalis*.

The fifth cleavage step shows another deviation from the decapod pattern in that the 2 macromeres derived from the lower medial octomeres divide radially, like their neighbors, rather than giving off new micromeres (Cf. Pl. 1, Fig. 5 z), so they really
 265 no longer show any special feature. This means that the anterior-to-posterior differentiation of the germinal disk does not yet occur, and the peculiar medial stripes (p. 146) are not formed. Otherwise a congruent feature is that the 2 medial macromeres of each side give off micromeres by formation of transverse furrows, whereas all the other macromeres divide radially.

The 32 cell stage (Pl. 24, Fig. 12) is thus composed of 4 new micromeres and 8 micromeres derived from earlier ones, plus 20 macromeres. The division of the older micromeres has been slightly accelerated (Fig. 11).

The *arrangement* of the blastomeres at this stage deserves special attention: at the 16 cell stage already (Pl. 24, Fig. 10), the central gap has been enlarged by an extension of the transverse slit on either side of the anterior and posterior micromeres, leading to the complete separation of the latter. Thus a central gap of considerable size is formed in which the micromeres dispose of some space (surrounded by the ring of macromeres). This space is further enlarged by a separation of the upper and lower macromeres along the medial line. Thus a rather loose cell complex is formed that apparently permits some deviations. The descendants of the first micromere generation in particular indulge in such deviations; they achieve virtually all the conceivable variants of arrangement, the two most common being those shown in Figures 12 and 13 of Plate 24. But even the macromeres vary in their respective shape and position, so that it is impossible to reconstruct the earlier cleavage conditions from later cleavage

patterns, i.e. find a precise preliminary condition for each variant observed; indeed one and the same picture may have been achieved by different ways, and *vice versa*. Cleavage continues to be very irregular, so that a strictly individual predestination of each cell is out of the question (p. 22).

Subsequent stages show germinal discs comprising a ring of macromeres (with an anterior and posterior, sometimes also lateral gaps: Pl. 24, Fig. 14) surrounding a loose, irregular arrangement of micromeres. The latter then become progressively more tightly packed around the central gap, which is generally transverse but highly variable; this condition persists in the dividing cell material to the end of cleavage (Figs. 15 and 16). At that stage, sometimes a little earlier or slightly later, the gap disappears completely. This closure generally marks the end of stage I leading to our organogenetic description.

266 Stage II. The formation of endomesoderm shows a striking difference in comparison to decapods (Pl. 24, Fig. 17 and Pl. 13). But no general statement is possible here since again there are some differences between *Octopus* and *Argonauta* (the latter being more similar to decapods, as shown in Plate 32). The thickened rim of the blastodisc is not smooth, it shows about 12 irregular, incompletely separated portions (similar to *Loligo*, see Pl. 1) that will subsequently fuse together. What is more striking, however, is the fact that the multilayered ring (light in the figures) lies indeed exactly at the periphery, the yolk cells (which formed an indistinct peripheral zone) having been drawn under the disc at the very beginning of germ layer formation. Extending rays seem to be completely lacking. On the other hand, the superposition of subperipheral cells over the peripheral ones (as shown in Textfig. 31 d) is certainly distinct in *Octopus*.

In other respects we find an obliteration of typical patterns of formation, as is characteristic for the whole octopodan development in comparison with decapods. It looks as if the gelatinous, amorphous condition, which originally warranted the designation "Malakia" for the adults, had its influence also on the developmental mode of the octopods.

Stage III. The multilayered marginal zone grows centripetally while the whole germinal disc grows slowly in overall size (Pl. 24, Figs. 19 and 20).

Stage IV (Pl. 25, Figs. 1 and 9) is 4 days old. One can now distinguish the thin, darker yolk envelope from the lighter embryonic body, which is ventrally (ml) slightly indented by the "posterior gap". Using this landmark, the germ is safely orientable.

In the center a darker spot (cl) persists; this is the last remainder of the unilayered zone around which the cell material is concentrated in preparation for the formation of the mantle rudiment. The germinal disc covers the animal pole of the egg like a cap.

At stage V (5 days old) the mesoderm is more strongly developed in the lateral parts of the embryonic body (Pl. 25, Figs. 2 and 10) and the germinal disk now covers about one fourth of the yolk mass, its edge cutting slightly into the yolk surface. The disk diameter is still less than the transverse diameter of the egg.

At stage VI (6 days old; Pl. 25, Figs. 3 and 11) the mesoderm concentrations become more distinct: the arm crown (ar) separates peripherally from the head anlage (au) and the gill area (km), and the mantle rudiment (ma) becomes very distinct; in its center the shell sac rudiment (se) forms. The latter becomes a circular epithelial plate (Pl. 25, Fig. 4), which slightly sinks down while an annular ridge rises as the rudiment of the shell fold at its periphery. For the moment one can see only a rather indistinct small depression (?shell gland?). The germinal disk now covers about one half of the yolk mass, the diameter of which is slightly less than the diameter of the embryonic anlage. The latter is largely represented by the yolk envelope, which grows rapidly.

267 Stage VII (7 days old; Pl. 25, Fig. 4; Pl. 26, Figs. 1-3) exhibits a similar aspect, but the differentiation becomes more distinct. The arm crown begins to subdivide into 4 portions representing 4 arms on either side; the third arm is stronger, the first more delicate than the rest; between the rather indistinct dorsal arm rudiments, the buccal area is visible as a transversally oval patch (mu).

Similarly, the gill rudiments (km), which are not yet distinct from the "waistband" (p. 104) and the funnel pouches, lie on either side of an area that represents the future anus (an). On the head anlage, the future eye rudiments (au) are barely visible.

The mantle rim (ma) begins to rise as a circular ridge, which is separated by a shallow depression from the thicker zone surrounding the shell sac rudiment, where the material of the fin rudiments is concentrated.

The yolk is now more widely covered; about 2/3 lie inside the embryo.

At stage VIII (8 days old; Pl. 25, Fig. 5; Pl. 26, Figs. 4-6), the folding processes start; the ocular folds and the buccal edge become distinct; the arm rudiments become equally prominent (Cf. page 272) as humps of moderate height. The funnel pouches (tt) become distinct as low edges on either side, and laterally from their lower ends the statocyst rudiments (st) appear as shallow pits. These lower ends of the pouch rudiments are typically connected by the "waistband" (gb) which is now distinct from the

gills. Between the arm crown and the waistband lies a rather broad, dark (thin) zone in which only later (p. 105) the funnel folds will appear (stage XI).

The mantle rim is now elevated as a bulgy ridge; dorsally the position of the lacking proostracum is marked by a shallow depression; the shell fold is contracted, so that only a small, slightly transverse pore marks the position of the rudimentary shell sac. To the left and right of it the fin rudiments form slight elevations. The yolk envelope is almost complete now. Only a small dome (do) exposes the original egg surface.

Stage IX (9 days old; Pl. 25, Fig. 6; Pl. 26, Figs. 7-9) shows the complete closure of the yolk envelope. The embryo now is subdivided into a typical yolk sac and a slowly contracting embryonic body, which is already demarcated by a slight constriction. The arm rudiments are very characteristically shaped, broad, blunt warts. On either side they form a regular row with shallow separating slits, each rudiment having a flat outer surface. Their broad form is reminiscent of the bipartite arm rudiment of the sepioids (Pl. 23); but it could well be that this broad, flat form is simply due to a purely mechanical factor, namely the tightness of the surrounding chorion (but see p. 146).

268 The dorsal arm rudiment directs a diffuse, rapidly tapering appendix towards the mouth; it will remain recognizable at subsequent stages (Pl. 26, Fig. 7) and may represent missing elements of the arm crown, especially the rudiments corresponding to the dorsal arms of decapods. The ventral, medial rudiment also must be mentioned; it probably represents a phylogenetic reminiscence of an earlier formation.

The mantle rudiment shows a similar aspect to the preceding stage; however, the ring of the muscular mantle, the darker zone it surrounds, the nearly closed pore of the shell sac and the fin rudiments are particularly distinct in their positional relationships, calling for a more detailed interpretation. The fin rudiments are strikingly large, and a considerable portion (p. 110) lies *behind* the transverse, poorly marked furrow that extends from the scar of the shell sac, thus passing over to the ventral side of the prospective mantle sac.

Below the dark zone on which the fins lie, one would expect to find the shell sac, to which the muscular mantle ring would be attached peripherally; this zone can be compared to the shell cone area of the oegopsids, the rather indistinct dorsal gap in the muscular mantle being a special representation of the proostracum. However, much like this dorsal zone which tends to become occupied by the advancing muscular mantle, the cone area also is replaced and the fin rudiments (Figs. 7 and 8) finally come to lie on the surface of the mantle muscle as in many decapods (p. 189).

The funnel tube folds (tr) are now distinct, though less so than the waistband; the statocysts grow deeper, the ocular vesicles contract to become closed. The buccal invagination (mu) sinks deeper, and in its middle part, close to the anterior border, a small depression marks the unpaired rudiment of the poison gland. The parts surrounding it are slightly convex and can be considered the rudiment of the subradular organ (Cf. Textfig. 127).

Stage X (10 days old; Pl. 25, Fig. 7; Pl. 27, Figs. 1-3) has the yolk sac more strongly constricted; the arm crown and the individual arm rudiments are contracted and take on characteristic shapes. The second and third arm rudiments begin on either side to prepare the covering of the eye, one rudiment being somewhat drawn out in the direction of the mouth, the other in the direction of the funnel. The third arm rudiment is connected by a small fold (at) on either side directly to the funnel base. This fold can be interpreted as the rudiment of an older Adductor infundibuli lateralis, as can be seen from the subsequent figures (stages XI and XII). It disappears later on (at least from the surface: see Pls. 28 and 29). The eye vesicles are closed, the posterior edge of the mouth is drawn forward while the poison gland rudiment has migrated posteriorly. The statocyst (st) is closed excepting a small pore; the funnel pouch has achieved its definitive union with the rather prominent funnel tube folds. The gill rudiments show a differentiation of the tip from the basal part (kh). The latter contains a blood sinus, which is the rudiment of the branchial heart and does not therefore belong to the actual gill rudiment. Medially between the gill rudiments the anal papilla has become distinct; in some preparations a transverse groove already marks the site of the anal opening that will be formed much later.

The mantle rudiment now is very prominent due to the beginning formation of the mantle cavity. Only one narrow dorsal strip interrupts this circular slit (Fig. 3). Here a primary connection persists between the head and the mantle rim. The dorsal mantle cavity can thus form only from a paired rudiment, since the slit advancing from both sides unites only secondarily below the mantle. On the ventral side, there is another medial interruption of the mantle cavity due to a small link (frenulum) that is formed as in all dibranchiates, connecting the muscular mantle rudiment to the anal area; here it is particularly well developed, similar to the sepiolids (p. 251). The connection indeed is the rudiment of the medial mantle septum, based on which a *Musculus adductor pallii medianus* also will develop here.

In an apical view of the mantle (Pl. 25) the aspect of the preceding stage is still recognizable. But the part of the fin rudiment that lies below the transverse furrow is now disappearing, whereas the upper part becomes more distinct, with the two lateral components now being joined medially. (This rather marked modification of the primary fin rudiment that can be interpreted only as a phylogenetic reminiscence. This is particularly surprising since the secondary form of the fin has no recognizable function, i.e. does not become effective).

Stage XI (11 days old; Pl. 25, Fig. 8; Pl. 27, Figs. 4-6) shows a rather modest progress in the direction taken. On the mantle rudiment, the embryonic fin differentiation reaches its maximum in the form of two transverse ridges that are joined above the sharply indented scar of the shell pore. From this junction, a faint ridge extends anteriorly, which may be interpreted as an indication of the anterior limb of Hoyle's organ, which is not differentiated in the typical form in octopods.

At this stage, the previously dark zone marking the shell part of the mantle sac is reduced due to the centripetally advancing muscular mantle tissue (p. 185); the replacement of the shell by the muscular mantle (as assumed for the phylogeny of octopods: Vol. 1, p. 657) is thus achieved in a "cenogenetically" shifted form. On the second and third arm rudiments, the basal extensions have become prominent and allow us to recognize the typical arm pillars (pf₂ and pf₃). The upper one lies, like a
270 wedge, between the eye and the dorsal arm. The lower one should not be confused with the earlier mentioned fold connecting the third arm with the funnel; this fold starts from the posterior edge of the arm pillar, as can be seen in Figure 8.

Actual eye stalks are not formed here; but the mass of tissue corresponding to them is very prominent on either side. As in decapods it is essentially composed of the rudiments of the white body. The buccal opening is strongly reduced due to the formation of a thin, hymen-like marginal fold, rather than to a contraction of the entire buccal edge; the latter shines through the thin membrane, which becomes closed, and will be the only structure figured for subsequent stages (Pl. 28).

The mantle edge has reached the medial ends of the funnel pouches dorsally and will overgrow them subsequently. Before that can happen, an intervening part of the dorsal surface (Pl. 27, Fig. 3; nk) apparently must be concentrated; in phylogenetic interpretation this reflects its degeneration. A similar process subsequently is taking place in the immediately adjoining zone (Pl. 28, Fig. 3: z).

We can interpret this as a reminiscence of a process in phylogeny by which the mantle (visualized also in its fully formed stage for each phylogenetic stage) became connected, in anterior direction, with the nuchal area in relation with the obliteration of the nuchal plate, in a way similar to what we observe in the sepiolid series *Rossia*, *Heteroteuthis*, *Stoloteuthis* (Vol. 1, p. 577). We can indeed imagine that from a stage like that seen here, the mantle rim would grow forward freely, perhaps combined with the formation of the anterior half of the nuchal attachment; we could then interpret stage XI as related to a phylogenetically preliminary condition (in the sense of our introductory considerations given on p. 40) by still expressing its rudimentary form.

The above process does not correspond from its very beginning to the nuchal band formation as achieved in adult Sepiolinae (Textfig. 105), behind which a typical, articulated nuchal connection could still exist. Instead the furrow (nk) in Figure 6 marks the deepest point of a dorsal mantle cavity, provided we are willing to consider a slight depression as such. The latter advances in octopods, similar to what happens in sepiolids (Textfig. 100), along with the mantle rim, entailing a similar morphology of this zone. Again an early fusion of tissues does not occur here; what actually happens is a shift of parts combined with the degeneration of that part corresponding to the posterior section of the nuchal attachment.

Stage XII (Pl. 27, Figs. 7-9) is 12 days old. The arm crown has made some marked progress: the dorsal arm now shows a distinct pillar (pf₁), which is derived from the lateral arm face, similar to what we have seen in *Sepioloa* (Pl. 23); here again (indeed already at the preceding stage, Fig. 6) the pillar base is separated from the medial arm face by a shallow depression. This phenomenon raises a problem: whereas in sepiolids
 271 the longitudinal furrow of the arm is derived from a paired rudiment, there is no such derivation in the present case; in contrast, it appears clearly that the brachial part providing the pillar also forms the back of the arm, in other words continues to respect the symmetry plate of the arm. This is indicative of transformations in earlier phylogenetic history that cannot be reconstructed in detail, because we do not know any dibranchiate precursors or any conservative descendants of them that might show a transitional state. In any case the back of the dorsal arm in both octopods and sepiolids must be derived from originally lateral, asymmetrically situated material.

The similarly shaped pillar of the second arm (pf₂) has become a narrow extension embracing the ocular mass dorsally. An identical arrangement is visible ventrally in the third arm pillar, to which the base of the fourth arm is attached in such a way that

an entirely independent pillar does not appear; even in decapods, the corresponding pillar (Pl. 17, Fig. 6) is not really distinct.

The funnel lobes become united medially to form the funnel tube; the posterior rim of the latter shows a retractor on either side (rt). More medially, on either side of the anal papilla, the roots (y) of the Adductor pallii medianus are recognizable (as in *Sepiola*). The dorsal mantle rim begins to join the funnel pouches more intimately. Otherwise the mantle rudiment does not exhibit any new feature; it is simply more elongate, but still cap-shaped, hiding the deeper parts of the enlarged mantle cavity with the insertion of the Adductor pallii and the posterior parts of the gill bases. The tips of the gills point progressively in anterior direction.

Stage XIII (Pl. 28, Figs. 1-3 and 7) is 13 days old. The arms are now slightly pointed appendages; their inner side shows the three larval suckers ($sn_{1,2,3}$). They are not of equal size; the size decreases distally, thus reflecting the typically sequential formation. Although the arm tip continues to grow in length, no additional suckers are formed up to hatching or in the earliest larval period. Sucker formation thus is interrupted for a rather long time; this is a typical feature of octopod development (Pls. 31, 37).

The arm pillars, especially the two dorsal pairs, have grown further across the head surface, following a slight furrow which marked their future way already at the preceding stage. On the medial pillar of each side a delicate, light longitudinal ridge has formed, continuing on to the outer edge of the dorsal arm; its correspondence to a glandular ridge of decapods is easily recognized (Pl. 23). A similar line runs along the lateral edge of the outer pillar. The parts lying medially from the longitudinal furrows of the dorsal arms has not participated in the formation of the arm pillars, and the buccal area occupies a broad zone separating these arms. In the periphery around the primary buccal opening or "outer lip", a bulgy inner lip (il) becomes visible.

272 In a lateral view, about one half of the ocular mass is embraced by the arm pillars. On the eye itself, the iris fold is now visible; it appears strikingly narrow.—The funnel complex is essentially complete, and the mantle rim grows towards it, thus preparing the closure of the mantle cavity. The gills have one branchial lamella (x) each. The dorsal connection of the mantle rim with the head appears broader due to a real fusion (Cf. p. 283) that progresses laterally along a fairly straight line (z). This fusion follows the base of the funnel pouches (tt), the free edge of which thus is overtaken by the mantle (at y), and continues to lengthen rapidly, limited by 2 corners that tend to approach the arm pillars (at dl).

The fin rudiments show another (the third) transformation (Cf. p. 283): they grow forward, in the form of slowly tapering ridges, on either side of the mantle sac and thus might indicate that the *Octopus* species in which the adult forms here show delicate lateral ridges or edges, or even broader seams, have conserved true fins in contrast to the present species where they completely disappear (Pl. 29).

Stage XIV (Pl. 28, Figs. 4-6) is 15 days old. (In an egg mass laid on a 19th May, the colder temperatures resulted in slower development, so that only stage X was reached after 15 days). Here the dorsal arm pillars, which can now be identified as head covers, have reached the dorsolateral mantle corners, with which they have become fused (z). Medially they are still separated by the broad mouth complex, which contains the buccal mass rudiments; this complex reaches medially to the mantle rim (y). The ventral head covers also have grown markedly, and both ocular edges (vk, dk) cover more than one half of the mass surrounding the eye and approach the eye itself.

The mantle sac has continued its development in the direction taken. Its nuchal fusion is much broader than before, the newly integrated lateral parts of the mantle rim now covering the funnel pouches; later on, they will become actually fused with the dorsal-most parts of the pouch. The ventral funnel rim also is becoming covered by the mantle edge. The fin rudiments have reached the culminating point of their new type of development (Cf. above).

The mouth is more deeply embedded between the dorsal arms, as if the latter strove for its inclusion between their basal parts; in an anterior view, it already shows the definitive arrangement (Pl. 28, Fig. 8).

At stage XV (18 days old; in the above-mentioned egg mass laid in May, only stage XII was reached after 18 days; cf. Pl. 28, Fig. 8, Pl. 29, Figs. 1-4), the mouth begins to be actually encircled by the dorsal arms, and especially by the parts lying medially from the longitudinal furrow. The mouth now shows the thin outer and thick inner lip more distinctly (Pl. 28). The yolk sac stalk is strongly constricted at its base by the arm crown, which allows the subsequent topography of the buccal field to be laid out. The larval suckers show a distinct depression marking the future suction chamber.

273 The posterior parts of the dorsal head covers have grown broader medially and laterally, now also showing the outer glandular lines (dl_s). The formation of the ventral covers has also made progress. The ocular edges of both the dorsal and ventral covers now surround the greater part of the ocular mass; the lower, posterior surface of the

latter (the cheek part) shows the olfactory tubercle (ro), which was barely visible at stage XIV. This tubercle approaches, but still lies at some distance from, its definitive location (Pl. 30).

The funnel edge now lies inside the mantle. The funnel tube shows a peculiar constriction (at x) lying between the olfactory tubercles; it can be interpreted as a primitive attachment complex, since at later stages the mantle rim will fit into this depression (Cf. *Argonauta*, Pls. 34 and 35).

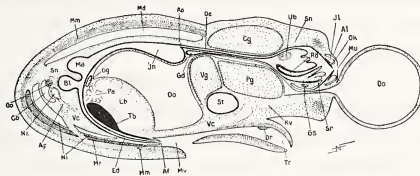
When the mantle cavity is exposed by dissection (Fig. 4 of Pl. 29), it shows a situation that is already quite different from the corresponding condition in decapods (Pl. 17): the anal papilla (an) lies very far anteriorly and the Septum pallii medianus (ms) has followed closely. It divides the whole mantle cavity into two distinct compartments. The gill rudiments show a typical surface differentiation; there are three gill lamellae on the ventral side. In contrast the branchial hearts are very voluminous, shifted laterally. The pouches lying behind them are not coelomic branchial heart pouches (they are lacking) but renal sacs, which never extend as far laterally and posteriorly in decapods. Close to the gills, nearly connected with them, lie the rudiments of the stellate ganglia (sg), which look like mantle swellings. This position, which is typical for the octopods (Cf. Pl. 8, Fig. 8), suggests that the (now lost) proostracum of the ancestral forms was extremely broad (Cf. Vol. 1, p. 104) and occupied much more than the nuchal attachment zone, in contrast to the situation in decapods having a narrow proostracum (Textfig. 60).

Stage XVI is 21 days old (Pl. 29, Figs. 5-8; Pl. 28, Fig. 9). It shows the primary lid fold essentially complete: the lateral edges have approached one another with their posterior extremities, which have become connected by a delicate integumental ridge, the so-called posterior connecting piece (hb). During this process, the olfactory tubercle (ro) has become separated from the eye, as is typical; this demonstrates that the connecting piece is derived from the intervening part of the ocular mass (the homolog of an ocular stalk).

The mouth and the apical zone next to it are now completely covered: the mouth (Pl. 28) already lies inside the arm crown and waits, and it were, for the final reduction of the yolk to take up its definitive position. Between the arms, velar membrane connections now appear distinctly. The arm tips begin to be drawn out into pointed ends. On the apex of the head, the glandular lines of the dorsal arms are pushed close to one another; between them lies an intervening stretch of head cover (x), which is

274 derived from the medial parts of the dorsal arms.—The mantle sac is considerably enlarged, pouch-like. The mantle cavity (Fig. 5) shows further differentiations: the stellate ganglia have moved away from the gills, but remain connected with them by the branchial bands. The gills are also further differentiated; in their outer (dorsolateral) edge the branchial spleen is distinct. Through the translucent tissues one can recognize the central heart (hz), auricles (vk) and the two branches of the vena cava (vs); the renal sacs (ni; m instead of ni in Fig. 5) extend almost to the rear end.

At stage XVII-XVIII (24 days old; Pl. 30, Figs. 1-3) the primary lid fold (pl) is



Textfigure 118. — Medial section of a nearly mature embryo of *Octopus vulgaris* (stage XIX-XX); 34× natural size. From Volume 1, page 666. The figure shows the typical topography of a young octopus. Cö: coelom (pericardium); Hz: heart; Ap: Aorta posterior; Ni: kidney; Ms: mantle septum; Ed: hindgut; Mu: muscular mantle; Af: anus; Mv: mantle cavity; Tb: ink sac; lb: liver; Pa: pancreas; Gg: Ganglion gastricum; Ma: stomach; Sn: blood sinus; Vc: Vena cava; In: Crop; Ao: Aorta anterior; Gd: poison gland; Oe: oesophagus; Vg: visceral ganglion; Pg: pedal ganglion; Cg: cerebral ganglion; Ub: lower buccal ganglion; St: statocyst; Kv: cephalic vein; Dr: funnel gland; Tr: funnel tube; Gs: sublingual ganglion; Sr: subradular organ; Rd: radula pouch; Il: inner lip; Al: outer lip; Ok: upper beak; Mu: mouth; Do: yolk sac (cf. Textfig. 116).

already considerably contracted, and the olfactory tubercle, which now lies far behind (ro), has taken up its typical position at the end of the mantle slit. The mantle sac has grown larger, so the embryo already shows a truly larval form. The fin rudiments have disappeared.

In the skin, chromatophores (ch) are now distinct, especially on the ventral side and at the bottom of the dorsal mantle cavity; in dorsal view the latter ones can be seen across the mantle.

Other skin differentiations are of more special interest: the rudiments of the setal sacs and setal tufts. In chromic acid and Zenker preparations, they can be seen as light rings already at stage XIV; they are in fact cup-shaped skin invaginations, the basal (lightly stained) cell of which secretes a spine; the latter will subsequently (Pl. 30, Figs. 4-6) grow beyond the pore of the sac like a short seta. Joubin (1892) has

described the formation of these structures, taking them for the chromatophore rudiments (Cf. Textfigs. 120 and 122 and Querner, 1926).

275 Stage XIX-XX is 28 days old (Pl. 28, Fig. 10; Pl. 30, Figs. 4-7). This is a fully developed larva; only the small yolk sac gives it an embryonic appearance: such stages can hatch from their envelope when stimulated, whereas they continue their development in the envelope for a few more days if undisturbed. Hatched animals achieve yolk resorption during free swimming. Such larvae are almost entirely covered with the integumental spines mentioned above; these are lacking only on the base of the funnel tube, on the funnel pouches, around the primary lid edge, on the arm tips and the inner side of the arms, and on the yolk sac. The latter is wrinkled, not smooth as figured somewhat diagrammatically.

The arms are short and stout, each with the typical three octopodan suckers and with a tapering, naked tip, which acts as a palp and forms the growth zone of the arm; the arms are connected by distinct velar membranes.

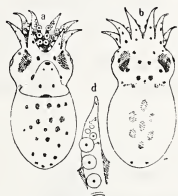
After removal of the small yolk sac, the mouth rapidly takes on its typical position in the center of the arm crown (Pl. 28); it is then tightly surrounded by a regular circle of 8 basal suckers, which functionally represent the buccal funnel of decapods.

The primary lid fold has contracted over the eye; only a moderately large, generally somewhat oval, elongate opening remains, which can further contract or dilate. The area surrounding it is a fully transparent skin which functions partly as a lid, partly as a cornea. Normally the opening does not lie above the eye lens, but rather behind it or dorsally from it; this does not seem to hinder the visual function.

The funnel apparatus now shows the pouches and the tube as typically shaped, distinct components; but the skin is so swollen (even at earlier stages) at the base of the funnel tube that the latter partly becomes engulfed by the head, only the tip remaining free. In preserved specimens, the funnel tube is shortened and stouter than the muscular tube itself, since the swollen skin again has an influence (Cf. Pl. 30, Fig. 7).

The mantle sac is somewhat egg-shaped, the body end representing the more pointed egg pole. The head mantle connection takes up the entire width of the dorsal side, whereas the ventral half of the mantle rim remains free. The olfactory tubercles lie in the far corners of the mantle slit; the mantle rim appears already directly connected with their upper edge (p. 260).

After dissection, the mantle cavity offers the aspect given in Fig. 7 of Pl. 30: on either side, the posterior funnel rim is drawn out into a sharp corner (te), on the inner side of which the funnel retractor (rt) inserts. A stellate ganglion (sg) lies on either side of the inner mantle surface, like a roundish swelling, connected to the anterior part of the visceral mass by a sort of ligament (z), which is the anterior mantle adductor. Anteriorly and laterally from it lies the paired entry to the dorsal mantle cavity (p. 260). The latter forms a blind sac extending far posteriorly, as shown in Textfigure 127; from the ventrolateral mantle cavity it is here separated by a thin septum (y), which breaks open only later so that the above-mentioned muscle then runs freely across the mantle cavity, as can be seen in adult octopods in general (?Cirroteuthoidea?).



Textfigure 119.



Textfigure 120.

Young life stages of *Octopus*, probably *O. vulgaris*, from the plankton of the Bay of Naples. 10× natural size.

Textfigure 119. — Dorsal and ventral view, and the aspect of the inner face of an isolated arm, which shows a clearly larval stage. Note the general similarity to the last embryonic stages, larger eyes and growing arms notwithstanding. The arms show the beginning of postlarval sucker formation (cf. Pl. 28), immediately in a zigzag arrangement. The whip-like end of the arm (6) is involved in grasping and functions as a palp. Inset 25× natural size.

Textfigure 120. — A rather poorly preserved, somewhat older specimen. The two insets show a part of the skin in profile (b) and one spine enlarged (c) (40× and 200× natural size, respectively).

On the posterior part of the visceral mass, the funnel retractors form prominent ridges extending to the base of the gills, where they become inserted to the mantle. Where this happens, the remainders of the shell sac lie on either side, containing the future "cartilaginous rodlets" that represent shell relics. Their essential function thus seems to be a strengthening of this insertion; we should indeed remember (Textfig. 55) that the typical insertion of these important muscles reaches to the shell sac and (the latter being the mediator) to the shell. So even here a trace of this correlation remains.

On the medial part of the visceral mass lies the typical anal papilla. The rectal part of the intestine is not free as in decapods (Cf. Pl. 7); it is embraced and thus hidden by the two muscular sheets that form the roots of the Adductor pallii medianus (ms_1). These roots extend rather far posteriorly, and their narrow insertion on the mantle still appears much like a septum. Subsequently the rear part of this septum breaks open (Vol. 1, Textfig. 385), so that this muscle also runs freely across the mantle cavity.—In front of the anal papilla, one recognizes the superficially located Vena cava (vc).

277 The gills still exhibit a rather typical structure, although the number of gill lamellae is fairly low, so that they appear relatively voluminous (Cf. Pl. 7). The gill attachment achieved by the branchial band (kb) reaches almost to the tip of the gill and extends to the posterior end of the stellate ganglion. The branchial hearts (kh) are prominent roundish bodies: they lie at the base of the gills, but not ventrally (as in decapods: Pl. 17); they are shifted laterally. The vein limbs (vs) and the lateral parts of the auricles (vk) leading to the efferent branchial vessel shine through the surface tissue. The lateral mantle veins are hidden; posterior mantle veins are entirely lacking along with the fins.



Textfigure 121. — "Metamorphosis" of *Octopus vulgaris*. Lateral view of a planktonic juvenile stage and of a benthic young animal. Both in swimming position.

a) Larva of Textfigure 119 in lateral view, $10\times$ natural size. For explanations see Textfigure 116.
b) Young animal; occurring in coarse sand or detritus in the coastal zone of the Bay of Naples, perhaps more frequently at greater depths (200 m).

It is not known how long the larval life lasts. I have been able to maintain hatched animals for up to 12 days in the aquarium, but I had no appropriate food for them other than hatchling *Argonauta* (Cf. Vol. 1, p. 678). But I doubt that they could be reared even under more favorable conditions. They are strikingly rare in plankton samples, and transitional stages following the condition shown in Textfig. 120 have never been identified.

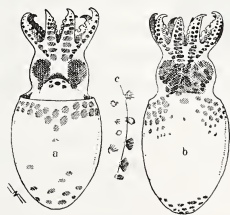
In contrast, young animals similar to those shown in Textfigs. 121b and 126 are rather frequently obtained. They are dredged up with sand, gravel and all sorts of

detritus and are easily raised on a corresponding substratum in the aquarium. They always bury deeply in such sediments or hide in narrow cavities, coming to the sediment surface only at night to forage (Cf. Vol. 1, pp. 677-679).

3. On the Embryonic Development of Other *Octopus* Species

The small eggs of mediterranean species of *Octopus* are all very similar to those of *Octopus vulgaris* (Cf. p. 71), except for minor differences in size that are of no significance in terms of developmental mode. I had no other egg masses at my disposal
278 for study. Only once an *Octopus defilippii* spawned in the aquarium under rather difficult circumstances, namely in a glass vessel of only a few liters volume, so that normal developmental conditions were not ascertained. The egg strings were similar to those of *Octopus vulgaris*, but they were not attached to a surface but were carried about in the arms by the anxious female; the egg strings thus became entangled with one another so that a single, ramifying festoon was formed.

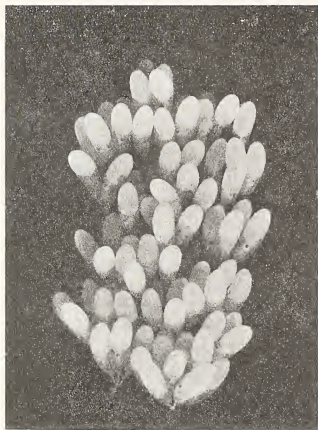
For exotic species of *Octopus* producing large eggs with a developmental mode similar to *Eledone*, see above (p. 262) as well as Tryon (1879, Pl. 19: *Octopus punctatus*), Rochebrune (1896: *O. digueti*) and Volume 1, page 686.*



Textfigure 122. — Larva of *Octopus macropus* from Messina. From Volume 1, page 668. The specimen is contracted due to fixation in formalin. Arm and funnel probably shortened as an artifact, the eyes are likely to be more prominent in life. However, the small head width is characteristic for this species, the planktonic phase of which is probably longer than in *Octopus vulgaris*. Despite the generally larval aspect of the animal, the suckers are already more numerous and arranged in 2 rows. 10× natural size. — The inset shows a piece of mantle surface in profile, with the spines split into tufts of setae. 44× natural size.

Among the larvae of the Neapolitan species, only those of *Octopus macropus* are easily recognizable and safely distinguishable (Textfig. 122); more advanced stages also have been identified and listed under this species in Volume 1, page 706.

4. On the Embryonic Development of the Genus *Eledone*



Textfigure 123. — Egg mass of *Eledone moschata*, fixed to a *Pinna* shell, which probably served as a hiding place for the spawning female, $2/3 \times$ natural size (cf. Korschelt, 1893, p. 69).

The eggs of *Eledone moschata*, which are spawned in small batches (Cf. Jatta, 1896, Pl. 7, Fig. 3), are rarely found in Naples, and as far as I know, they never form large egg masses. Personal reports about such egg masses have arrived several times from the Aquarium of Rovigno, where the conditions for maintenance or rearing of fully mature animals seem to be better. Korschelt (1893) described and figured *Eledone* eggs collected from the sea (Textfigs. 123 and 124).

The individual egg capsules are extremely large, measuring about 15 mm without stalk; they are laid in groups of 2-4 eggs. The embryo contained in the chorion measures about 13 mm including the yolk sac (Textfig. 124); an estimation of the original size of the undeveloped egg and its capsule would be 10 and 12 mm, respectively. Thus they can belong only to this species, as already indicated by Korschelt, since the otherwise similar eggs of *Eledone cirrosa* must be much smaller (See below).

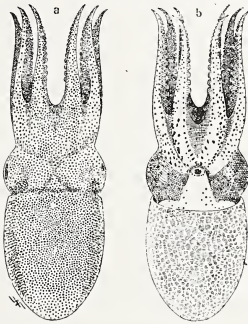
* Scientific Editor: It is interesting that Naef does not mention his earlier remarks on *Octopus* species producing large eggs (page 292 of Volume 1): "We consider as related to *Eledone* the Octopodidae represented by *O. digueti* de Rochebrune 1896, i.e. forms with regularly biserial suckers and with eggs which are 5-9 mm long (usually about 6 mm without capsule). (...I propose the name *Paroctopus*, type species: *P. digueti*, for these species.)"



Textfigure 124. — Embryo of *Eledone moschata* from the egg mass of Textfigure 123. Drawn after the original figure by Korschelt (1893, p. 72), slightly simplified. 5× natural size.

This barely half-grown embryo shows a condition later than the larval phase of development (which probably is no longer distinct).

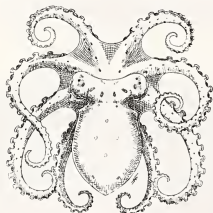
Similar egg masses have been collected several times in the coastal zone of Rovigno, where they were found beneath large stones, inside old containers or similar hiding places at shallow depths. Professor Dr. Cori kindly provided a series of eggs from such a sample, some of which contained nearly mature hatchlings, as well as newly-hatched animals, one of which is shown in Textfigure 125 (See also Vol. 1, Pl. 10, Fig. 1).



Textfigure 125. — Newly-hatched *Eledone moschata*. From Volume 1, page 676. 5× natural size. Note the arm and chromatophore development achieved beyond the larval stages of typical octopodids, the overall aspect being similar to that of an animal-like in Textfigure 121 b. The arms are strongly contracted due to formalin fixation and thus appear unnaturally short.

It is very regrettable (as in the case of *Rossia*, p. 247) that the embryonic development of *Eledone* has not been studied in greater detail. Although it is likely to show some atypical features (flattened germinal disc) related to the large yolk mass, one can expect, given the greater cell numbers or sizes, to find some formations earlier and more distinctly than is possible in *Octopus vulgaris*. The suppression of the larval stages (Cf. Textfigs. 119-121) must be an atypical feature. Conditions that can be considered homologous to a larval stage are essentially achieved already at the stage shown in Textfigure 124, which can be called XIX-XX: the arms are markedly elongated and show the general shape of arms in postlarval stages of *Octopus*. Each of them carries more than a dozen suckers. In contrast, the yolk sac is still much more voluminous than the embryonic body and is

about one-third longer than the latter (including the arms). From the figures it is not clear whether rudimentary fins are present as "lateral ridges" on the mantle (p. 287). One would tend to suppose that they are lacking, since they are not visible in the more advance juvenile stages (Textfig. 125), apart from the fact that it is not really certain that these ridges are conserved fin rudiments.



Textfigure 126. — Young *Octopus vulgaris*, drawn from life. $3\times$ natural size. From Volume 1, page 679. Note the attitude of the arms, the web, the prominent eyes, the funnel tube pointing to one side (the orientation being able to change). This is the typical aspect of a small octopodid.

The development following the stage shown in Textfigure 124 should be characterized by growth in size and histological differentiation of the different parts. The most striking feature is the lengthening of the arms. They appear too short in Textfigure 125 (due to fixation-related shrinkage). When alive they must have been very similar to the young benthic stages of *Octopus*, except for the arrangement of suckers. The latter are set in single file, corresponding to the primary condition of rudiments. Some 20 suckers can be recognized under a magnifying lens, and the outermost tip already shows the condition of Textfigure 51.

The overall aspect of the young animal in dorsal view must have been similar to the young octopus of Textfigure 126, which is therefore reproduced here once more. The tendency to roll the arms spirally and to
281 raise the eyes by muscular contraction and blood retention in the head probably is common to all young octopodids and to the adults of small species.

To my knowledge, eggs of *Eledone cirrosa* have never been observed in Naples, mature females ready to spawn only very rarely. I suppose that this species retires to greater depths or even to a different area for spawning, at any rate hiding away more regularly than the preceding species.

Joubin (1888) described unidentified *Eledone* egg masses, which must belong to *E. cirrosa*, which (judging from the ovary of mature females) has smaller, more numerous eggs than *E. moschata*. They were laid in short strings, essentially like those of *Octopus vulgaris*, the stalks of 5-17 eggs being glued together in a collective stalk, which in turn was glued to a substratum by an irregularly shaped fixating plate. The substratum in this case was the wall of the aquarium, above 30 cm above ground and

25 cm below the water surface; the egg strings were laid scattered, not in a large mass. There was no egg care; on the contrary the eggs were regularly eaten by the female if not protected from her. Individual egg capsules measured 7-8 mm in length, whole (long) strings about 40 mm.

The development was not observed, although the eggs were probably fertilized (since mating had been seen); this material could have been used for embryological work.—Jatta (1896, Pl. 7, Fig. 5) probably figured a postembryonic stage of this species. But as no scale is given, an *Octopus* stage similar to our Textfigure 120 cannot be excluded.

CHAPTER 13

The Embryonic Development of the Argonautids

Contents: 1. Generalities. 2. *Argonauta argo* (p. 299). 3. *Ocythoe tuberculata* (p. 313). 5. *Tremoctopus violaceus* (p. 317).

1. Generalities

Up to the present, no detailed description of the embryonic development of argonautids has been given. Some indications and figures were published by Kölliker (1844), who observed embryos of both *Argonauta argo* and *Tremoctopus violaceus* (see p. 317), and by Appellöf (1899), Korschelt and Heider (1893), and Steinmann (1899). The latter authors observed only *Argonauta argo*.

282 As for myself, I had *Tremoctopus violaceus* and *Ocythoe tuberculata* at my disposal; but I cannot give a complete description of the development of these species; I will limit myself to giving some data and consider some developmental stages in comparison to corresponding ones of *Argonauta*.

A common feature of all argonautids is an ovoviviparous reproduction, i.e. the eggs are fertilized inside the body of the female and are laid only at more or less advanced stages, rarely before the end of cleavage. This condition contrasts with all other known dibranchiates that have been studied in this respect. An internal fertilization could be expected in other octopods as well, in which the spermatophores are

placed in the distal oviduct during mating; it might even occur in the spiolids where the spermatophores are attached close to the genital pore of the female, but according to my observations, it does not occur. In all other instances, the eggs are in fact laid at an immature stage.

The early development also differs considerably from that of other octopods (*O. vulgaris*), as will be seen in *Argonauta*. But true family characters appear only at more advanced stages: a solid attachment is formed between the mantle and the funnel corners, the latter being curved forward to sit in corresponding depressions of the former (Pl. 31). The mature embryos or young larvae show a striking overall aspect, with an almost egg-shaped outline, and the arms surrounded by a peculiar sleeve into which they can be retracted more or less completely (Textfigs. 128 and 132).

A more important feature is that the shell sac rudiment is formed in the typical way, but soon begins to degenerate (especially after its closure) and finally disappears altogether (Textfig. 127). But there is no basic deviation from the typical course of development, neither in this nor in other organogenetic processes; thus the typical development of octopods in general could be described based on argonautid development as well as on that of *Octopus vulgaris*.

2. The Embryonic Development of *Argonauta argo*

Cleavage of *Argonauta* eggs takes place inside the long, meandering oviduct (Vol. I, p. 776), which functions as a uterus; sometimes even endomesoderm formation starts before the eggs are released. On the other hand, I have seen egg masses in which 283 the blastoderm formation was barely completed; the moment of laying does not apparently correspond to a precise stage of development, but generally it appears to occur between stages I and II (Pl. 32).

The material at my disposal did not allow me to study in detail the eggs still contained in the oviduct; before I knew of the ovoviviparous condition of this species, I had preserved *in toto* the only mature female that could have served for such a study (which of course would require an appropriate treatment of the eggs). This is regrettable, since the early development probably differs from that of *Octopus vulgaris*, as suggested by the subsequent stages described below. However, this gap will easily be

filled in the future. One simply has to take the contents of the oviduct from a freshly caught, mature female, to study and preserve them in portions progressing from proximal to distal parts of the oviduct. One should thus obtain a fairly complete series of stages.

State I: the youngest embryos observed in spawned eggs show the aspect of Figures 1 and 5 in Plate 32; at close inspection they show a unilayered blastoderm. But this picture is very different from the corresponding *Octopus* stages (Plate 24). A distinct gap (x) marks the center, at the site corresponding to the "central plate" of a decapod blastoderm (Pls. 1 and 13); here the layer of cytoplasm covering the yolk is very thin, completely devoid of nuclei. From this central gap, a linear, more narrow gap extends to the periphery of the blastodisc; it is reminiscent of the "medial band" of homologous decapod stages. There is no doubt about the descendance of this peculiar formation from lower medial octants corresponding to what occurs in decapod cleavage. That the central gap is so conspicuous here is probably related to the very rudimentary condition of the shell sac in argonautids. It is indeed the shell sac rudiment that absorbs the cell material of the central area of the blastoderm in other dibranchiates (pp. 105,146 and 161).

These peculiarities of the *Argonauta* embryo allow one to orientate it at early stages already, in contrast to what is observed in *Octopus* (p. 280). They are still perfectly distinct at stage II (Pl. 32, Fig. 2); subsequently the linear medial band disappears, while the central gap persists. Much as in *Loligo*, the central plate can be observed up to the formation of the shell sac, and there can be no doubt about its derivation from the corresponding part, i.e. from the cells formerly surrounding the central gap (Pl. 33). But in other respects also the youngest germinal disc studied differs from corresponding *Octopus* stages: whereas the latter (Pl. 24) have a rather smooth rim, the blastoderm of *Argonauta* shows peculiar spikes (dz) which seem to correspond to the rays observed in similar stages of decapods (Pl. 13). It is not rare that they continue into single cells situated more distally, the only difference from decapods (Textfig. 65) being the scarcity of such radial yolk cells. Each spike essentially consists of one such cell, which is of particular aspect and continues to remain recognizable: it is flat and shows a strongly flattened nucleus that appears very large in an apical view. But other cells also participate to the base of these extensions.

Subsequently a typical, multilayered ring (vr) is formed inside this series of spikes, and the latter are drawn in below this ring at the outset of the following stage.

Stage II (Pl. 32, Fig. 2) shows this rather broad, well-developed ring which is closed except for the lower, medial gap. The multilayered zone enlarges continuously thus reducing the central, unilayered part which finally coincides with the central gap shown in the picture (Pl. 32, Figs. 3 and 4). During the same time, the yolk mass becomes progressively covered (Figs. 6 and 7) while the differentiation of the mesoderm is in preparation.

Stage VII (Pl. 32, Figs. 8-10) shows these mesoderm concentrations quite distinctly: the arm crown (ar), the buccal area (mu), the cephalic anlage and the ocular zone (au), the waistband (gb) and the gill rudiments (km) are recognizable as light patches; the mantle rudiment (ma) begins to rise. In apical view it shows an important aspect (Pl. 33, Fig. 4): in the center the shell sac rudiment appears as a circular depression. It is surrounded by a barely raised, yet distinct rim, from which a small shell fold will arise. This depression lies within another depression, which is less well defined, but roughly cross-shaped; the three upper branches may be compared to the inverted T-shaped scar of decapods (Textfigs. 36 and 37). This pattern is due to the unequal centripetal progression of the cells inside the muscular mantle rudiment; they indeed advance in four lobes.

It cannot be overlooked that the shell sac rudiment appears rather sizable when one considers its outline. But it is not made of a solid epithelium; there is only a relatively modest number of flattened, frail cells that already suggest a degenerating condition.

Stage VIII (Pl. 32, Figs. 11-13; Pl. 33, Figs. 5) shows the rudiments of the arms (I-IV), mouth (mu), eyes (au), statocyst (st), funnel complex (tt, tr), gills (km) and mantle (ma) in an arrangement known from *Octopus* (Plate 26), which is basically identical to the pattern observed in decapods. The positional relationships between these rudiments does not show any surprising features. What is special is the general positional relationship of the whole embryonic body and the yolk mass: the figures clearly show the yolk mass almost entirely surrounded by the embryonic body, so that the yolk envelope (dh) is very reduced in size, quite reminiscent of the form
285 observed in oegopsid embryos (Pls. 8 and 9). The embryo figured had almost entirely enclosed the yolk mass, and the yolk envelope showed only a small circular opening (ks) which would have been closed shortly. The yolk sac represents an inconspicuous dome, which is surrounded by the arm crown in a very typical fashion, however.

As in the case of oegopsids, this condition is due to the small amount of yolk (*Argonauta* eggs are the smallest cephalopod eggs so far observed), on the one hand, and to mechanical factors acting inside the embryonic body, on the other hand; the latter are related to quite normal properties of any such stage: it is indeed a general feature that at early stages the embryo encloses more yolk than at the subsequent stages when the body progressively contracts. This contraction extrudes part of the yolk so that the outer yolk sac grows relatively larger. Along with this extrusion, the constriction of the yolk sac base begins (See p. 176).

The arm crown shows the typical 4 rudiments on either side and ventrally a doubtful arm rudiment. It is drawn backwards markedly, similar to what has been seen in oegopsids (Pls. 8 and 9). The rudiment of the mouth is quite isolated and exhibits the poison gland rudiment (gd) in anterior position. The funnel lobes (tr) are barely recognizable, the statocysts (st) form shallow pits with a slightly raised rim, the funnel pouches are fairly distinct, ridge-like elevations. The waistband (gb) is still more conspicuous than the funnel lobes and forms the anterior border of the dark zone (with few cells) in which these lobes arise.

The mantle rudiment follows the pattern known from *Octopus*: it is surrounded by a distinct mantle furrow except for two narrow medial interruptions, one dorsal and one ventral. Dorsally the furrow never forms since the nuchal attachment of the head persists; ventrally the rudiment of the mantle septum (ms) blocks a deeper penetration of the mantle cavity.

In apical view (Pl. 33, Fig. 5), the shell sac rudiment has contracted into a transverse oval limited by a distinct edge, which is the small shell fold.

Stage IX (Pl. 32, Figs. 14-16; Pl. 33, Fig. 9) shows an enlarged, more prominent yolk sac area (do), the arm rudiments raised as round papillae. The buccal edge, ocular folds and statocysts are now contracting. The poison gland rudiment (gd) is shifted backwards. The funnel lobes begin to rise and to make contact with the funnel pouches. The gill papillae (km) are more distinct; between them the anal papilla arises in the form of two slight elevations, the furrow corresponding to the future anal opening (an), whereas the elevations themselves will form the two lips.

The apical view of the mantle rudiment (Pl. 33) shows a strongly contracted shell fold forming a transverse, nearly slit-like opening, from which distinct lateral furrows extend on either side, similar to what happens in *Sepia* (Textfig. 37), whereas the dorsal one remains diffuse and the lower one disappears almost completely. Below the

shell sac pore, there is not a spacious shell sac as in the decapods, which are more complete in this respect, but only a shell sac rudiment barely larger than the pore itself, i.e. a transverse, narrow little sac lined with a frail epithelium of progressively degenerating cells, which will completely contract and close at the following stage (Fig. 10 of Pl. 33, see also Textfig. 127a).

Stage X (Pl. 33, Figs. 1-3 and 10) shows a more distinct yolk sac, which nevertheless appears very inconspicuous when compared with similar stages in *Octopus* (Pl. 27). The arm rudiments are now more prominent, and the third pair shows the typical positional relationship with the funnel tube, though not as distinctly as in *Octopus* (p. 282). The ocular folds are closed; the posterior buccal edge is drawn forward while the poison gland progressively shifts backwards. The pores of the statocysts become narrower; the funnel lobes (tr) and funnel pouches (tt) join to form the funnel complex.

The bowl-shaped mantle rudiment (Fig. 10) shows the shell sac pore practically closed. The shallow, somewhat gutter-shaped dorsal part (x) forming the nuchal connection broadens slowly. It thus approaches the funnel pouches; this appears like a compression of the rather indistinct zone which forms the nuchal attachment in decapods (Pl. 16). This can be interpreted as a reminiscence of a phylogenetic process, namely degeneration of the nuchal attachment, for which no cellular material is made available (Cf. Textfig. 99).

At stage XI (Pl. 33, Figs. 6-8) the yolk sac begins to constrict: the arm rudiments grow longer and basally form the arm pillars, as particularly visible in lateral view. They begin to surround the eye complex in the typical fashion. Since they are surprisingly well differentiated in *Argonauta*, I have figured their development with special care. As is usual, the ventral arm does not show a really distinct pillar. The dorsal arm pillar belongs to the part lying laterally from the freshly formed longitudinal furrow, whereas the medial part conserves a relationship to the mouth area via a tapered extension that was more distinct at the previous stage.

The mouth itself shows a phenomenon already mentioned from *Octopus*: a delicate skin fold derived from the buccal edge, a sort of hymen, closes the otherwise wide mouth opening and leaves only a narrow pore. But this is not the end of the process in *Argonauta*: the closure is soon completed due to further growth of the fold. The embryonic gut is thus completely closed, as the anal opening forms only very late. The buccal complex developing below the skin faces the yolk sac (Textfig. 127); it looks as if the latter were tied to the mouth. This condition lasts up to the larval stage: only the

hatched larva frees its mouth of this peculiar muzzle by simply ingesting the remaining yolk sac, which by that time has grown rather small. It can be found inside the crop 12 hours after hatching.—Supposedly this behavior is common to all argonautids. At any rate, the mouth is closed in the same way in *Tremoctopus* embryos (Pl. 31).

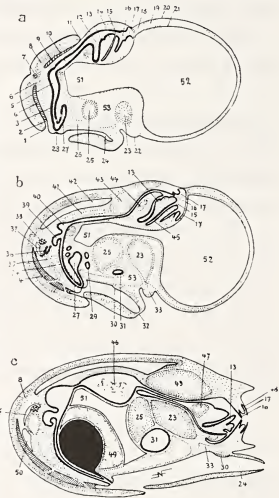
Textfigure 127. — Diagrammatic medial sections of two embryos and a newly hatched larva of *Argonauta argo*. 55× natural size.

a) Stage XII. The mantle is cut at slightly lateral level to show the remaining shell sac (7), which is already degenerating in the middle plane, and the mantle cavity (4 and 9) in its full extent. (In the middle plane, the ventral mantle would appear, and the dorsal cavity would be taken up by the solid nuchal connection between the mantle and head). The funnel is also shown in a slightly lateral section, so the position of the opening is not clearly visible. Note the bulging buccal mass (12-17), the closure of the mouth (18), the yolk sac (52) and the anal papilla (28). (62× natural size).

b) Stage XVI. The dorsal mantle cavity has been formed by fusion of the paired lateral cavities. The shell sac has disappeared. The mantle edge has caught up with the anal papilla and the posterior edge of the funnel, the outer opening of the funnel tube will soon form. (54× natural size).

c) Stage XX. Newly-hatched larva, aged 24 hours. The yolk sac has been ingested (46), the mouth is now free. One recognizes the outer and inner lips (17 and 48), surrounded by the arm crown (only the web being cut in the middle plane). (50× natural size).

1: ventral mantle rim; 2: medially open mantle cavity; 3: hindgut; 4: mantle septum; 5: embryonic stomach; 7: shell sac rudiment; 8: muscular mantle; 9: dorsal mantle cavity, growing to the middle plane from either side; 10: foregut; 11: dorsal mantle edge; 12: radula pouch; 13: tongue; 14: subradular organ; 15: opening of the poison gland; 16: beak rudiment; 17: inner lip; 18: closed mouth; 19: dorsal yolk sac vessel extending anteriorly and laterally; 20: ectoderm of yolk sac; 21: yolk epithelium; 22: medioventral part of arm crown; 23: pedal commissure; 24: funnel tube; 25: visceral ganglion; 26: Vena cava; 27: ink sac; 28: anal depression; 29: ink gland; 30: funnel organ; 31: statocyst; 32: closing membrane of funnel tube; 33: Vena brachialis; 34: posterior communication of vein limbs; 35: Aorta posterior; 36: heart; 37: pericardium; 38: gonad; 39: caecum; 40: stomach; 41: Aorta anterior; 42: dorsal mantle cavity; 43: cerebral ganglion; 44: lower buccal ganglion; 45: poison gland; 46: crop; 47 = 44; 48: outer lip, i.e. reopened buccal edge; 49: liver; 50: kidney sac; 51: remainder of inner yolk organ; 52: outer yolk; 53: origin of Vena cava.



The eye vesicles now bulge and show an iris fold rudiment. The statocysts are closed; the funnel lobes unite to form the tube. The funnel retractors appear where they join the funnel pouches. The ventral mantle edge still exposes the branchial and anal papillae. The anal papilla, which is still strikingly large but correspondingly flat, will soon contract, but will remain visible for a considerable length of time. The

position of the prospective opening is a distinct transverse groove (Textfig. 127 a). The dorsal mantle edge begins to cover the funnel pouches, which then become connected with it and thus are pushed down into a slight depression. On its outside mantle shows a transverse furrow indicating the position of the shell sac rudiment, which is clearly recognizable in histological sections (Textfig. 127 a); it will soon divide into two diverging tubules or cell clusters. The cells are indeed not solidly attached to one another to form an epithelium, so the whole complex could easily be overlooked even by a keen observer; it is the basic correspondence with the more distinct rudiment of *Octopus* that allows one to recognize it. At later stages, this identification becomes impossible; the remaining, loosely connected cells disappear in the muscular tissue of the mantle. But even here it appears clearly that the last recognizable site is related to the insertion of the funnel retractors to the mantle (p. 133).

Stage XII (Pl. 33, Figs. 11-13, Textfig. 127 a) shows the yolk sac fairly constricted below the more elongate arm rudiments, each of which now has 3 (2-3) roundish, slightly flattened tubercles, the sucker rudiments. The arm pillars have expanded on the head surface both dorsally and ventrally, so that about one half of the ocular mass is anteriorly surrounded by the primary lid rudiment now forming, which shows three distinct components: the dorsal and ventral ocular edges of the arm pillars and the connecting middle piece.

The apical head surface also exhibits three distinct zones: the ocular masses on either side, which represent the eye stalks of decapods and carry the laterally bulging eye vesicles, and in the middle the slightly convex surface, which hides the buccal mass rudiment, as can be seen in a medial sagittal section (Textfig. 127). The position of this rudiment is still superficial. The surface aspect of the apical field is dominated by two shallow furrows, in which the arm pillars will move further backwards.

The funnel tube is now closed due to complete fusion of the funnel lobes, i.e. the anterior opening is also shut (Cf. p. 112). The small window (tö) marking its position is very narrow and so indistinct that it is easily overlooked even in histological sections. But it is always there; in other words, the wall does not simply close down on the entire funnel surface. The mantle rudiment is cap-shaped, still showing a transverse furrow on the outside. Below its outer epithelium lies the shell sac (Textfig. 127) in the form of a transverse, narrow canal the lateral ends of which are better developed (being wider and composed of more cells) than the medial part; the latter is now disintegrating. The ventral mantle edge is growing over the gills, pushing the anal

papilla anteriorly; the dorsal mantle edge shows a broadening fusion with the head, in the form of a transverse suture as in *Octopus* (p. 285); it continues to expand (Cf. Textfig. 45). The extremities form distinct angles on the mantle rim and partly cover the funnel pouches (tt).

Stage XIII (Pl. 34, Figs. 1-3) shows the result of further growth of the arm rudiments and arm pillars. The dorsal ones are very distinct and advance towards the mantle rim angles mentioned above, whereas the ventral ones become more broadly connected to the sides of the funnel tube, into which they will later grade without any sharp demarcation. It should be remembered that the funnel tube is a likely appendage of the arm complex (p. 104); thus we see a mere enforcement of relationships between the ventral arm and funnel tube rudiments that existed from the outset. The truly funnel-shaped end of the funnel tube shows a peculiar transverse depression (Fig. 2 x) by which it is separated from the posterior edge and funnel pouches; its significance becomes recognizable only at subsequent stages. More clearly than in *Octopus* (Pls. 28 and 29) it corresponds to the future position of the contact area with the mantle rim. It looks as if the mechanical action of this contact had been inherited, as if this phenomenon were due to the differentiation of an exposed funnel part with a typically swollen skin next to the remaining thin skin with a smooth epithelium, which should be compressed by the apposed mantle musculature. Such a shallow (essentially neolamarckian) explanation must of course be rejected definitely and vigorously. The parts are simply appropriate within the structure and context of the whole; how this is achieved is not so easily detectable. At this stage already the posterior funnel corner, which will later form the characteristic connection with the mantle, begins to project on either side of the anus. The gill rudiments sink in the progressively deepening mantle cavity; the anal papilla contracts markedly. Anteriorly and laterally to the papilla, the roots (y) of the Adductor pallii medianus become recognizable; its posterior, unpaired part lies in the deep part of the mantle slit.

Stage XIV (Pl. 34, Figs. 4-6) is markedly more advanced. The dorsal arm pillars have reached the mantle rim and become attached to it at x. This attachment begins in the lateral parts where the funnel pouch lies underneath (p. 287). The medial part of the mantle rim touching the head first remains free; its secondary connection to the head covers is slowly completed only at subsequent stages. The funnel tube shows the seam now complete and beginning to disappear; there is no longer a medial indentation in the posterior rim. It is closely joining the advancing ventral mantle rim; but in

290 the rounded notch the anal papilla is still visible. The mantle sac is considerably enlarged and completely hides the gills. A lateral view shows that the funnel pouches reach dorsally into the mantle cavity, and that three quarters of the ocular mass is encircled by the arm crown. The olfactory tubercle (ro) is now distinct at the posterior end of the ventral ocular ridge (vk); it forms an inconspicuous, oval, flat wart, which already had been recognizable as an epithelial thickening at the preceding stage. It is visible also in the ventral view and shows the same position as in *Octopus*, which is clearly different from that typical for decapods (Pl. 5).

Stage XV (Pl. 34, Figs. 7-9) shows the further enlargement of the arms, each of which has 3 suckers with distinct rudiments of the suction chamber as the sign of a definitive feature. Distally to the last sucker, a free tip appears as the rudiment of the subsequently formed parts of the arm; before that differentiation begins, it forms a palp-like appendage (Pls. 35, 36). The ocular edges encircle the ocular mass more thoroughly; the ventral edge (at v) has closely joined the olfactory tubercle, in preparation of the subsequent exclusion of the tubercle from the orbital chamber (as in other dibranchiates, in which the vicinity between the eye and the olfactory tubercle is less striking, although the primary relationship, already demonstrated by *Nautilus*, is recognizable in all instances). The dorsal head covers also have become broader both medially and laterally. The posterior end of the ocular edge (d) has remained close to the end of the mantle slit which has come closer to the olfactory tubercle as a result of the continued fusion of the head with the mantle. The medial apical part of the head, which hides the buccal mass, i.e. the part not yet covered by the head covers, becomes progressively limited in extent.

The funnel is now fully surrounded by the mantle rim; only a minor part of the posterior notch is visible ventrally. The mantle rim is approaching its definitive position, i.e. the transverse furrow of the funnel pouch, while the olfactory tubercles are pushed laterally due to the development of the head covers. The funnel tube begins to become markedly enlarged; only its tip remains free, whereas the rest is covered by the broad connection with the head covers.

Stage XVI (Pl. 35, Figs. 1-3) is close to the formation of the corneal fold. The posterior end of the ventral edge (which has just passed the olfactory tubercle) and the posterior end of the dorsal ocular edge (which is now lying in front of the end of the mantle slit) have approached each other, leaving only a small distance between them; but the future connection has not yet materialized. Whereas the posterior ends of the

ocular edges are closely applied to the ocular mass, the remaining parts are separated from it by an anteriorly deepening slit, so that the ocular mass already shows a tendency to sink into the mass of the arms, thus preparing the formation of the deeper parts of the orbital cavity.

291 The parts of the head covers derived from the different arm pillars are still distinct, dorsally in an apical view, ventrally at least in histological sections. They will subsequently fuse with one another so that a distinction in a surface aspect becomes impossible. The area of the buccal mass (sm) is still largely exposed in a dorsal view, i.e. the head covers have not yet come together medially and thus have not yet fully replaced the primary cephalic epithelium. The olfactory tubercle (ro) is now very distinct, in contrast to earlier stages where it was barely distinguishable, and in contrast also to the subsequent stages where it will become more indistinct, partly covered due to its relation to the mantle slit.

The posterior funnel edge is in its definitive position, and the funnel edges become rapidly anchored on the inner surface of the mantle, by first bending slightly outwards (as is typical for octopods) in correspondence to mantle depressions that (at the next stage) will become deep pits, opening posteriorly. Thus an attachment complex typical for this family, absent in others, will be differentiated. Anterior to the mantle pit, a small tubercle is recognizable. As early indications, these formations (tubercle, pit, and bent funnel corner) can be found already at stages XIV and XV (Cf. also Pl. 31, Fig. 6 and Pl. 36, Fig. 5).—The mantle sac has a roughly hemispherical shape, the ventral rim occupying the predetermined site on the funnel surface. The tubercles and pits can no longer be seen from outside, whereas in stage XIV they were still distinctly visible.

Stage XVII (Pl. 35, Figs. 4-6) shows an annular primary lid fold: immediately anterior to the olfactory tubercle, a delicate skin fold has arisen and formed a connection between the posterior ends of the ocular edges of both head covers. It is not distinct from these edges, and the points of fusion can be determined only approximately from a comparison with the preceding stages (between XVI and XVII). The ocular masses are further retracted into those of the arm crown, thus progressively forming the conditions for closure of the orbits.

In the dorsal aspect (Cf. Pl. 29) modifications have arisen rather suddenly: the head covers of either side have become united medially, along the whole median line, from the mantle rim (nt) to the fold connecting the dorsal arms (sh), which is the

rudiment of the interbrachial web. This anterior section is of purely integumental nature; the typical muscular mass of the head covers is lacking here, so that this part appears darker (translucent) in the preparation.

The delicate transverse furrow, which separates the buccal mass anteriorly from the yolk sac, is conserved. It must be considered as the location of the mouth, which thus lies anterior to the arm crown, a reminiscence of the typical molluscan snout (pp. 32 and 64).

292 The arms are more strongly differentiated and have grown some in length. The length differences typical for the family become distinct, especially the acceleration of the dorsal and the retardation of the lateroventral arms. The mantle slit is now complete, the olfactory tubercle being situated at its end on either side. This situation seems essentially achieved by the shifting of the tubercle itself, but in part also by the progressive fusion of the mantle rim with the dorsal head covers and the head. The mantle sac is further enlarged and approximately equals the head in volume; it will soon grow larger than the head.

At this and the preceding stages, the body surface is no longer completely smooth: the mantle, funnel tube, head covers and the basal parts of the arms show delicate tubercles, providing an impression of "goose-pimples". Each tubercle is due to a flask-shaped invagination that forms a bulging, subepithelial vesicle, inside which the larval spines arise (p. 289). These vesicles already contain the rudiments of the spines, but the latter break through the skin only at the end of embryonic development.

Stage XVIII (Pl. 35, Figs. 7-9) shows no striking modification of the surface aspect other than the beginning contraction of the primary lid folds above the eyes, which thus appear to sink into the cephalic mass. The unequal arm lengths become increasingly marked, as is the relative size increase of the posterior body part compared to the anterior one. The entire embryo approaches the final aspect of the mature embryo, more drastically so at the next stage.

Stage XIX (Pl. 36, Figs. 1-3; Pl. 37, Figs. 2 and 3). The yolk sac now is an insignificant appendage with very limited contents and with a thick wall; during swimming this yolk sac is easily carried by an artificially freed embryo. The embryo is indeed viable outside the egg capsule; strong stimuli lead to its hatching from the egg, and these slightly premature hatchlings behave like fully developed larvae. The arms, especially the dorsal ones, are markedly longer than the others; especially the whip-like end is elongate. A low, but regularly developed web connects the arm bases; it is

stronger between the 4 dorsal arms than between the ventral ones. The lid folds are contracted above the eyes except for a moderately large, variable opening that can be closed almost completely.

The funnel is enlarged, the funnel tube being superficially distinct from the pouches. The funnel mantle connection approaches more closely the definitive situation in that the part of the funnel corner (y) adhering to the mantle tubercle (Pl. 37, Fig. 2: kn) becomes distinct by a projecting rim as in decapods. Thus a situation typical for the genus is achieved; it does not occur in other argonautids. The firm connection thus formed is also expressed in the slightly projecting corners of the ventral mantle rim (Pl. 36, Fig. 2: te).

293 These embryos show the first chromatophores in a characteristic distribution: they are very scarce and are situated according to the following pattern: (1) a group of 5-7 chromatophores at the posterior end, (2) a series of 3-5 along the medial part of the free mantle rim, (3) two pairs on the funnel tube, (4) one on each side behind the eye, close to the funnel pouch, (5) two pairs on the dorsal head surface, anterior to the fused mantle rim, (6) one above each eye, (7) one on each arm base, appearing somewhat later than the others, (8) a group of 8-10 at the bottom of the dorsal mantle cavity, visible across the translucent mantle.

Plate 37 shows the mantle cavity of this stage after dissection. The ventral aspect shows also the construction of the funnel complex, especially the characteristic formation of the funnel rim with the bent funnel corners (te), the upper section of which is taken up by the bowl-shaped funnel attachments (kn) with their prominent rims. On the backside the typical funnel retractors (rt) insert here; they form muscular ridges extending posteriorly to the base of the gills. The stellar nerves (x) form similar ridges more laterally, leading to the deeply situated stellate ganglia (sg) which represent very large swellings on the inner side of the mantle. The gills (km) are strikingly underdeveloped, with only two lamellar rudiments each. The lateral edge of the gill is attached by a weakly developed branchial band (kb) leading to the stellate ganglion in front, as is typical for the youngest octopod stages. A bulging skin area behind the gill accommodates the branchial heart (kh). The mantle septum (ms) is still complete, very thin posteriorly, distinctly muscular (ad) anteriorly. It reaches close to the typically shaped anal papilla. The ink sac (tb) is visible behind these structures, the vena cava (vc) more anteriorly. Inside the funnel tube lies a typical, tripartite funnel gland. In front of the stellate ganglion, one can see the communication with the dorsal mantle cavity,

which is fully exposed in Figure 3.—We see here a wide cavity between the visceral complex—and the mantle, the stellate ganglia (sg) being visible at the bottom on either side, separated from the visceral mass by a delicate furrow; the surface of the visceral complex shows a number of large chromatophores, as is typical for octopods.

In the fully developed larva, the gills are slightly larger, and the mantle septum is often perforated posteriorly, so that the ventral mantle cavity is also in one piece. Later on, the deep part situated between the gill and the stellate ganglion also becomes perforated, thus forming a further communication with the dorsal mantle cavity on either side; at the present stage, it is still closed by a thin membrane.

294 Stage XX (Pl. 36, Figs. 4-6; Pl. 37, Fig. 1) represents the fully developed hatching, which shows features of a larva. The yolk sac is nearly completely resorbed, the remaining small amount (not figured here) is simply ingested as it lies in front of the mouth, thus closing it (Textfig. 127); its fragments can be found inside the crop (46 of Textfig. 127 c).

The arms are further enlarged and are now strikingly unequal in length, the dorsal ones stronger and longer, the lateroventral ones shorter than the other arms. The web connections show a peculiar feature, as in other argonautids (Textfig. 132): it looks as if the web (including the outer arm skin) were stiffened, so that it remains in place when the arm axes contract, thus forming a sort of cuff that is conserved even at more advanced, postembryonic stages (Vol. 1, p. 767). It is the structure of the skin in this area that must be responsible for the formation of this "cuff". The skin is indeed thin and smooth on the inner surface and on the distal parts of the arms, whereas here it is swollen and contains several histological differentiations, such as the flask-shaped glands producing the integumentary spines. The arms can be more or less completely retracted into this cuff. The funnel and the mantle sac are further enlarged and the mantle outline essentially determines the ovoid shape of the young animal. The latter shows the characteristic overall aspect of juvenile stages of this family, as can be seen from a comparison with Textfigs. 130 and 132. The mantle sac, the distal part of the funnel tube, the head (except for the immediate surroundings of the edge of the primary lid), and the outside of the "cuff" now exhibit the tips of the integumental spines which have broken through the skin, all of them being orientated anteriorly.

The spread out arm crown is shown in Figure 1 of Plate 37. Here we see the typical conditions of an octopod larva. In the center we see the thick inner lip and the thin outer lip; inside the opening of the inner lip lies the edge of the lower beak. This

buccal area is slightly elevated in a sort of buccal cone, which is surrounded by the arms. The arms consist of a rather evenly developed basal part carrying three suckers and a distal part whose unequal development creates the differences in arm length; the distal part is smooth or covered with delicate wrinkles, and tapers to a rather pointed tip. The basal parts are connected by web sectors, which here show typical octopodan features, inserting on the outer arm edges.

Although the distal arms are longer than the other ones, they are not otherwise distinguishable, neither superficially nor in their finer structure; there is still no hint of their prospective role as broodshell arms. There is also no trace of the glands that will later produce the (brood) shell; this is easily understandable, since the arm parts present are not yet those directly related to that shell at later stages (See Vol. 1, pp. 767-775!). The surface aspect does not yet allow one to distinguish male and female individuals; there is no hint of the striking dimorphism that will appear later.



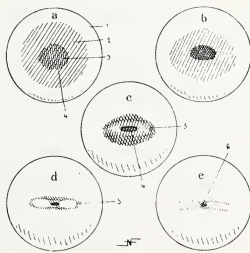
Textfigure 128. — (From Vol. 1, p. 765). Newly-hatched juvenile stage of *Argonauta argo*. 30× natural size. For comparison see the youngest larvae of *Tremoctopus* (Textfig. 132) and *Ocythoë* (Textfig. 130); note the relative arm lengths and the closing complex of the funnel which is detached and exposed due to the slight outward curvature of the mantle rim. Note the following typical features: the cuff-shaped web of the arms, the small eyes which point slightly ventrally and anteriorly, and the oval primary lid, the few chromatophores, the glittering, rarely splitting spines which are recognizable only on the dark body surfaces, the large, flat olfactory tubercle, the dorsal suture of head and mantle, the funnel tube and the funnel pouches, and the insertion of the funnel retractor at the funnel attachment.

It must be emphasized once more that *Argonauta* has a small but distinct shell sac rudiment corresponding to the typical feature of octopods, especially of the poly-podoids; Appellöf (1899) has simply overlooked this rudiment. There is no point to the idea that secondarily the shell epithelium could have “returned” to the outer surface of the mantle. This has to be remembered when assessing the indication by Steinmann, according to which the first rudiment of the *Argonauta* shell is produced by the mantle.

3. *Ocythoë tuberculata*

Jatta (1896, p. 201) reported that he found nearly mature embryos, ready to hatch, in the oviduct of *Ocythoë tuberculata*. Unfortunately he did not provide figures, nor was this precious material preserved; since this species is very rarely found in the Bay of Naples, I had given up hoping to study its development. It was pure chance that on April 11, 1916 I obtained a mature female, freshly caught near Capri; it is described on pages 753 and 754 of Volume 1. However, this individual was not yet fully grown; perhaps the season was not quite favorable either; whatever the reason, I found the distal parts of the oviducts empty, and the stages recovered from the more proximal sections ended at about stage XII of *Argonauta*. In the extremely long oviduct, which acts as a uterus, the eggs are lined up in successive stages, but the progress is not continuous but stepwise, probably due to the mechanisms of fertilization; so an absolutely complete series could not be obtained even under more favorable conditions.

Unfortunately the time available did not allow me to study in detail the material obtained, and since the more interesting later stages were missing, I refrained from giving it priority. Furthermore, the embryos were dead and had to be preserved at once, so a detailed study of the fresh material was impossible (apart from the other



Textfigure 129. — Apical view of the mantle rudiment at stages VII to XII in *Ocythoë tuberculata*. 30 X natural size. Slightly diagrammatic. Stage VII (a), VIII (b), IX (c), X-XI (d) and XII (e).

Note the progression of the muscular mantle (1) in centripetal direction, the originally large size of the shell sac rudiment (3) and the progressive contraction of the shell fold (4) which is drawn out laterally, as is typical for octopods. Note also the formation of distinct fin rudiments (5) similar to those of *Octopus* (25) from the cell material lying on either side of the shell pore (6). 2 marks the gap in the center of the muscular mantle, which is not taken up entirely by the shell epithelium; in b (cf. Pl. 37, Fig. 8) is seems to provide a hint of a proostracal rudiment.

reasons mentioned). It turned out later that the preserved eggs were not exploitable for a study of cleavage; thus the gap remaining in the description of *Argonauta* development cannot be filled. I will simply describe a few stages in comparison to those of *Argonauta*, with emphasis on the development of the shell sac and related parts, since they are of special interest (Pl. 37).

The eggs of *O. tuberculata* are markedly larger than those of *Argonauta*; they resemble, in both size and (elongate) shape, the eggs of *Octopus vulgaris*. They measure 0.9×2.0 mm. As is typical for octopods, each egg is contained in a tough chorion, with the posterior end directed outwards (Textfig. 19); at the opposite side, the chorion is drawn out into a hollow stalk (that has no function here).

The early stages are similar to those of *Argonauta* (Pl. 32), whereas the more advanced stages clearly show genus-specific features.

Textfigure 129 shows the mantle development (Cf. Pls. 37 and 33). Let us consider first its special features, which have already provided interesting data (p. 256):

At stage VII (Textfig. 129 a; cf. Pl. 32, Figs. 8-10), the apical (posterior) view of the mantle cap shows a thickened marginal ring that contains the material for the mantle muscle. It surrounds a slightly concave field, in the center of which the shell epithelium is distinct. The latter is characterized by the fact that it is slightly depressed and closely applied to the yolk, which is visible as a darker mass. Furthermore, its cells have a different aspect. This part is still of considerable extent and thus reminds one of the picture seen in corresponding decapod stages (Cf. Pl. 15). But here a particularly striking feature is the wide separation between the shell sac rudiment and the muscular mantle rudiment (Cf. p. 270). The shell is represented twice, as it were: (a) by the area of the primary shell epithelium (3), which is surrounded by the (indistinct) shell fold (4), and (b) by the shell gap (2) of the muscular mantle. The concentration of both in the same narrow space is only secondarily achieved, in the position representing the fin and shell rudiments on the apex of the mantle sac, i.e. at the prospective posterior end. It is only then that the fin rudiments are situated on the outside of the shell (i.e. the shell sac), at the rim of which the muscular mantle is inserted as in the decapods. This condition is possible only after strong shifts of proportions (Cf. Textfig. 30) in both systematic-morphological (hence phylogenetic) and ontogenetic terms. The heterochrony in the various partial processes of ontogenesis strongly obscures the conserved reminiscences of the phylogenetic process (Cf. pp. 39, 40, 270).

At stage VIII (Textfig. 129 b) the muscular mantle has grown larger and has advanced centripetally in four parts, from the right and left sides above, and from the right and left sides below (Cf. Pl. 33, Fig. 4). This results in a progressive limitation of the dark shell gap, the integumental membrane of which (morphologically) belongs to the (poorly developed) shell fold that should grow over the shell epithelium. The latter also contracts and shows a slight indentation in the upper rim that could perhaps hint at a proostracum (See Pl. 37, Fig. 8). This process continues with the subsequent stage.

State IX: the shell sac invagination is more distinct due to the stronger elevation of the shell fold, in which some cellular material has accumulated on either side of the pore, indicating the formation of fin rudiments that will become more distinct subsequently.

Stage XI thus shows a morphologically significant condition: the muscular mantle rudiment now closely approaches the shell sac, on which its insertion is histologically differentiated. Since this formation is so small here, one would rather say that the shell sac and any shell rudiment it might produce are embedded in the muscular mantle, which closes down around it (See Textfig. 127 a). The opening of the shell sac now is a very narrow, transverse slit leading into a minute transverse cavity. On either side the fin rudiments now become rather distinct. They occupy the entire remaining, slightly concave, central field of the mantle rudiment.

At state XII, this central field disappears altogether, the muscular mantle having reached the shell sac while the shell pore closes down.

Clearly, these processes are similar to what we have seen in *Octopus* and *Argonauta*, and which can be surmised for *Tremoctopus* as well, although I have not been able to observe them in detail there. The small size and low number of cells in embryos of *Argonauta* must be the reason why the fin rudiments are so poorly developed there, whereas other differences might be due to more accidental modifications of the developmental process that could be devoid of any systematic significance. For example, the very distinctly four-lobed advancing edge of the muscular mantle in *Argonauta* (Pl. 33, Fig. 4) does not necessarily require a special phylogenetic interpretation.

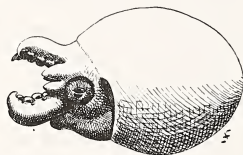
Let us now consider two stages of *Ocythoë* in greater detail:

Stage IX (Pl. 37, Figs. 4, 5 and 8) is similar to the corresponding stage of *Argonauta* (Pl. 32), but here we see stronger differentiation of details, as could be

expected in a larger embryo which is made of a greater number of cells. Thus the characteristic longitudinal furrow (y) of the dorsal arms already appears at this stage, whereas in *Argonauta* it appears much later (Pl. 33), and the statocyst (st) shows a peculiar sculpture. In another aspect, however, the embryo appears markedly retarded, the yolk sac envelope being still incomplete. This fact is doubtless related to the larger yolk mass, as is the larger relative size of the yolk sac, which gives the whole embryo an overall aspect more similar to *Octopus vulgaris* at the homologous stage (Pl. 26) than to *Argonauta*.

The embryonic body is also different in outline from that of an *Argonauta* embryo; it appears more concentrated, as can be seen from Plates 32 and 37. Specific features related to the definitive condition are observed in the unequal arm rudiments: the dorsal and ventral arm rudiments are already markedly larger than the lateral ones, the latero-ventral arms being most retarded. Thus each arm rudiment from the outset is allocated the mass of material corresponding to its prospective significance (as a counter-example, see Pl. 23).

Otherwise the figures show typical rudiments: it is noteworthy that the lateroventral arms are connected to the funnel by a ridge (at), as has been seen in *Octopus* (Pl. 299 26); that the ocular vesicles are almost closed, leaving only a pore; that the poison gland rudiment lies still in the center of the buccal edge, etc.



Textfigure 130. — The youngest known postembryonic stage of *Ocythoë tuberculata* (a female); 15× natural size. From Volume 1, page 750. Note the general similarity with Textfigures 128 and 132. Characteristic are the proportions of the arms (although they are strongly shrunken due to formalin fixation).

Stage XII-XIII (Pl. 37, Figs. 6 and 7) is quite similar to the corresponding stage of *Argonauta*, although the overall aspect is quite different due to the greater size of the yolk sac. The above-mentioned differences in arm development continue to be conspicuous. The cephalic section shows only one peculiarity, namely the mouth (mu) still being open. The buccal edge is strongly contracted, so one can surmise that the

subsequent development is similar to what we have seen in *Argonauta*, i.e. complete closure. Indeed *Tremoctopus* (Pl. 31), a more remote form, shows the same feature, so we can consider it as characteristic for the whole family. The dorsal arm pillars (pf) already extend posteriorly on the dorsal head surface, but they are less distinct in relation to the arms than is usual.

The funnel complex comprising the tube (tr), the pouches (tt) and the retractors (rt) shows the typical aspect; likewise the gills and the anal papilla are very similar to what we have seen in *Argonauta*. The mantle rudiment is bowl-shaped, already fused dorsally with the head (dm). The mantle organs are described above (p. 315). On the whole, *Ocythoë* exhibits (apart from some special features of the arms) the developmental type of *Argonauta*, but with more complete differentiation (fin rudiments); it is thus of special interest for the assessment of that genus.

4. *Tremoctopus violaceus*

Tremoctopus violaceus has not been observed in the Bay of Naples for many years, and since the time of Jatta, no mature females have been found; they might still be caught occasionally in Messina.

To the best of my knowledge, the egg masses of this interesting species have been
300 observed alive only by Kölliker (1844) who reported on them as if they were well-known material, without giving a detailed description of its development. Fortunately I have been able to study his material, so that I can give some indications about the embryology of *Tremoctopus*.

When looking through the collections of the Zoological Museum in Munich, I found a jar containing cephalopod eggs without further indications; at first sight I took them to be *Argonauta* eggs, since the embryos and capsules looked so similar to this genus (Vol. 1, p. 736). Closer inspection confirmed that part of the egg masses were indeed those of *Argonauta*, whereas the bulk contained embryos with different features, the older stages being clearly those of *Tremoctopus* (Pl. 31). Moreover these eggs were attached to peculiar bodies, which looked almost like pieces of coral that would have been preserved along with eggs attached to them. But closer inspection and a comparison with Kölliker's indications led to a very different opinion: these



Textfigure 131. — Egg mass of *Tremoctopus violaceus*. $1/2\times$ natural size. From Volume 1, page 742. See the text for details of collection.

The eggs are similar to those of *Argonauta argo*, but are markedly larger; for the embryonic stages they contain see Plate 31! They are at very different stages of development, similar to what is observed in the eggs deposited by *Argonauta* in its brood shell. As in the latter, the stalks of the egg envelopes are interwoven and glued together to form a cluster, the common stem of which is then glued, together with others, to the egg carrier, which represents the brood shell of *Argonauta*. A brooding female probably has two such egg carriers. According to Kölliker they are held by the dorsal arms and thus carried around, probably wrapped in the web.

bodies are egg carriers produced by the spawning female; the eggs are attached to them (much like the *Argonauta* eggs when they are attached to the inside of the shell) and thus are carried around by the female (Vol. 1, pp. 742, 778, 782).

The eggs are enclosed in the typical chorion capsule and differ from *Argonauta* eggs essentially by their size only. They measure 0.9×1.5 mm. Since this material is very old and did not contain all the stages, a complete study and description of development was impossible; I therefore describe only a few stages, the morphology of which is fairly straightforward (Pl. 31), for example, one that corresponds to:

Stage XI-XII of *Argonauta* (Pl. 37, Figs. 1 and 2; cf. Pl. 33), to which it is so closely similar that there can be no doubt

about a very close relationship. (But the family identification is in fact more securely based on the following stage.) Such an embryo can only be an argonautid! It is similar to *Argonauta* (but not to *Ocythoë*) in that the yolk sac is very small, though slightly larger than in *Argonauta*.

As has been seen in *Ocythoë*, the characters of the genus appear early, although in an apparently subordinate point, namely in arm proportions: already at this stage the third arm rudiment is strikingly retarded in terms of size, and the second arm rudiment clearly is less developed than the first and fourth ones. Thus from the outset each rudiment receives a mass of formative material corresponding to the future volume (Cf. Pl. 23). In any detail there is a high similarity of all parts with the corresponding ones of *Argonauta* embryos. Thus the mouth is completely closed as in *Argonauta*, and the yolk sac is tied to it. The mediodorsal part of the mantle rim is fused with the head in the typical fashion, and the outside of the mantle shows an aspect similar to *Ocythoë* (Textfig. 129 e). The shell sac is closed and the site of closure barely recognizable as

a small pit. Fin rudiments are situated on either side of this pit; they are less distinct than in *Ocythoë*. The figures provide details of the respective states of different rudiments. So far as the available material could tell, the early stages of development show the same features as corresponding stages of *Argonauta*; but an analysis of cleavage stages and early germinal disks was not possible.

Stage XVI (Pl. 31, Figs. 3, 4 and 7) already is rather different from corresponding stages of *Argonauta*; it shows the generic features very clearly. This is especially true in the arm crown development: the dorsal arm pair is markedly more advanced than the other arm pairs, the lateroventral one being almost rudimentary (See Vol. 1, Textfig. 440!). Web connections are recognizable between all the arms; in the two dorsal pairs they are sizable, thus underscoring a feature of the genus.

The unequal size of the arms is also reflected by the number of suckers (Pl. 37, Fig. 7): the lateroventral arms have only one sucker each, whereas all the other arms have the typical three larval suckers; the third sucker on the first arm is markedly larger, on the second arm it is smaller than the others. On the first arm there are two small additional sucker rudiments distally, emphasizing the accelerated development of the first arm pair.—Between the arm bases, in the center of the arm crown, lies the yolk sac stalk (*y*) below the mouth, which is completely fused with the yolk sac, as has been said earlier. Removal of the yolk sac exposes the outer and inner lips (*al*, *il*).

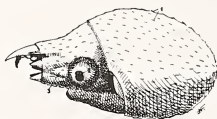
Formation of the corneal fold is not yet complete (*dk*, *vk*); the olfactory tubercle (*ro*) lies in its typical position, as in *Argonauta* (Pl. 35). The mantle sac shows the same shape as there, and its rim is dorsally fused (*x*) with the head in almost its entire width. The funnel tube is more slender than in embryos of *Argonauta*. The surface of the mantle, funnel tube, head covers and arm bases shows slightly elevated structures, as in *Argonauta* (p. 309), the little warts from which the integumental spines will emerge later.

Stage XIX (Pl. 37, Figs. 6 and 8) is again more closely similar to the homologous stage of *Argonauta* as far as the overall aspect is concerned. The yolk sac is strongly shrunken, the arms have grown in length without changing the relative size relations. The same is true for the sucker equipment of the arms. But the whole arm crown is now contracted so that the 8 proximal suckers form an almost complete circle around the mouth area. Within the latter, the yolk stalk (*y*) is regressive compared to the mouth and will soon disappear completely once the yolk sac remainder has been ingested. The larval suckers are functional, typical octopod suckers; their size relationships have remained the same as before (p. 319).

In the head section, the corneal folds are now formed and almost entirely closed; the remaining pore is surrounded by a zone in which the integumental spines (elsewhere rather densely set) are absent. The funnel shows the corners in a peculiar form (Fig. 6, te): there are no distinctly demarcated, cup-shaped attachments; the corners are simply bent outwards and thus insert into the slit-shaped pouches on the inner surface of the mantle.

The organs of the mantle cavity are essentially similar to what we have seen in *Argonauta* (Pl. 37); but the stage is more advanced in the differentiation of all parts: (1) the gills show 7 distinct gill lamellae on the ventral side; (2) the Septum pallii medianum is perforated in its posterior part, so that the *Musculus adductor pallii medianus* crosses the mantle cavity freely; (3) the dorsal and ventral mantle cavity communicate not only in front of and beside the stellar nerves, but also medially and posteriorly from these nerves, since the septum behind the stellar nerve has become perforated (See p. 260). All the integumental spines have broken through the skin surface; they are more numerous than in *Argonauta*.

Stage XX (Pl. 31, Fig. 5; Textfig. 132) shows a newly-hatched animal, which probably left the chorion at the very moment of fixation (Cf. p. 141). (Such larvae were numerous in the present samples, along with a considerable number of empty chorion capsules.)



Textfigure 132. — Newly-hatched *Tremoctopus violaceus*. 30× natural size. From Volume 1, page 736. Cf. Plate 31. The egg mass from which this animal was taken (or had hatched) apparently came from Messina; it belonged to the material described by Kölliker; it is now housed in the Bavarian State Collections in Munich. Cf. also Textfigure 131. Note the similarity with *Argonauta* larvae (Textfig. 128). 1: integumental spines; 2: primary lid; 3: lateroventral arms, becoming hectocotylized in the male.

The overall aspect is typically that of very young, ovoid argonautids. The young animal is indeed very similar to a young *Argonauta* (Textfig. 128); even the arm proportions are similar, disregarding that the fourth arm is slightly longer than the second 303 arm. This is particularly distinct when one considers the size of the last sucker (Pl. 31, Fig. 8). Here we see again a feature approaching the pattern observed on *Ocythoë*; it

is clear that the three genera are related in various respects (in terms of similarity or commonality of characters).

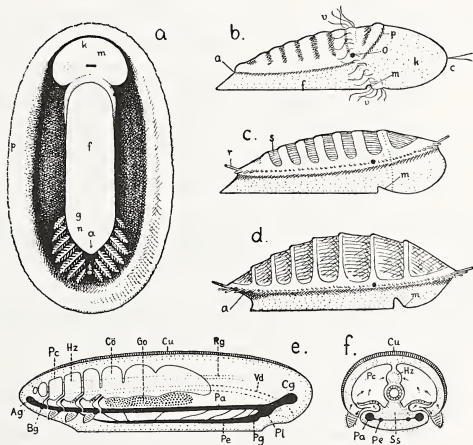
In preserved larvae the arm bases are always hidden in a cuff, as in *Argonauta* (p. 313), a feature that must be considered typical for the youngest argonautids. Often all the arms (especially the lateroventral ones) except the dorsal arms (Pl. 31) are completely retracted into the cuff, the arm tips being bent inwards. The head-mantle connection appears particularly broad.

The set of spines in the skin reflects the situation described above for stage XIX; the mantle cavity also shows the same conditions. The skin appears somewhat swollen and gelatinous, similar to what is observed in *Argonauta*, somewhat more strongly expressed.

These aspects should contribute to a more comprehensive view of the family, emphasizing its natural unity. The developmental pathways of *Tremoctopus*, *Ocythoë* and *Argonauta* appear as variants of a special octopodan type of development, which is not represented in a pure form in any one of the three genera; each of them indeed shows very peculiar specializations.

III. CONCLUDING SECTION

Since the above considerations always proceeded from the general to the specific, in other words were deductive in orientation (in contrast to the study proper), they



Textfigure 133. — Figure illustrating the archetypal conditions of outer body features in molluscs, and their morphological and phylogenetical interpretation. (Detailed explanations in Textfigure 10). e, f) Protomollusc, or an ideal transitional stage between a protoannelid and an archemollusc. b, c, d) Developmental stages of a placophoran mollusc that correspond to developmental stages of the protomollusc, if the shell plate rudiments are replaced by a continuous cuticular formation, and if the pedal sole is shortened so that it does not reach beyond the anal area. The spines on the mantle rim probably are comparable to the setae of annelids. a) Prototype of a placophoran form, seen from below. The picture shows the archetypal features of a mollusc, which might have had even more numerous pairs of gills with a corresponding coelomic outlet homonomous to the genital (g) and nephridial pores (n).

308 already contain a comprehensive order of the facts. A concluding synopsis can therefore provide no more than an ultimate, brief overview and emphasis on the essential points leading to an increase in our knowledge.

A source of special satisfaction for the author was the clarification of our ideas about the *archetypal body forms* of the *Mollusca* in general (pp. 69 and 105), of the *Conchifera* in particular (p. 117), gained in the course of this comparative study. This provides a solid starting point for the morphology and phylogeny of cephalopods, something that was hitherto wanting. This starting point is expressed in Textfigure 133, which will speak for itself (Cf. Textfigs. 7, 10 and 17).

An archetypal feature of the *cephalopods* (including the tetrabranchiates) is the very yolky egg and the resulting *blastodisc* development with a special yolk organ (p. 97) and an outer yolk sac; moreover, the subdivision of the pedal rudiment into a multiple crown of appendages ("arms", Textfig. 25), and their particularly strong concentration in the functionally anterior body section ("headfoot"). Subsequently, the latter undergoes a very peculiar, secondary complication and shifting of parts:

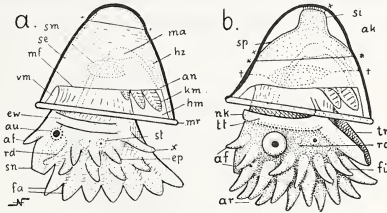
In each arm, the basal part becomes distinct and extends posteriorly (apically) across the head surface, thus replacing most of the primary head cover. These so-called "arm pillars" surround the eyes like a protecting wall, except on the side facing the mantle. The snout part of the head sinks, in posterior direction, into the mass of the arm crown, until the mouth comes to lie in its center, being surrounded by a special circle of small "buccal arms". The primary head surface remains exposed in the 3 most important *sense organs* (eye, olfactory tubercle and statocyst), the rest being enclosed by parts of the foot.

The primary eye is a stalked or at least very prominent eye ball with an excavation (pin-hole camera). The olfactory organ originally shows the form of a flat papilla with a sensory epithelium. As is typical for the *Conchifera*, the statocyst is formed from a sensory pit, which becomes invaginated and soon loses its open contact with the skin. From the primary *buccal rim* ("outer lip") a special formation of the stomodaeum ("inner lip") emerges; it later appears as the actual limit of the mouth.

The "*funnel tube*" rudiment appears as a relatively late formation derived from the posterior part of the foot; it consists of two lobes that bend medially and become connected to one another along the midline. They are secondarily connected with the apparently independent, heterogeneous, older rudiment of the "funnel pouches", which arises as a ring-shaped structure on either side of the middle or neck part of the

309 conchiferan body; it apparently does not belong to the cephalopodium, for which it provides the posterior limit. This formation cannot correspond to the *epodium* of gastropods, if the funnel tube is considered homologous to it (See Naef, 1911, p. 83).

For the latter homology, we have no real demonstration either. But it is obvious that the funnel tube rudiment is derived from the dorsal side of the posterior foot extremity, thus occupying the position of those parts of the gastropod foot that carries the operculum. In the earliest cephalopod ancestors (which might be as remote in time as the common ancestor of all conchiferan molluscs) the funnel pouches must have been represented by a *fold* that closed (and regulated) the *entry of the mantle cavity*. It is questionable whether this role was purely protective or served also respiration or even locomotion.



Textfigure 134. — Ideal protoconchifer (a) and hypothetical *Nautilus* or protocephalopod embryo (b). For detailed explanations see Textfigures 25.

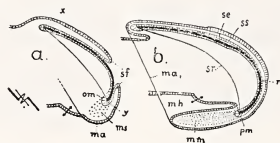
Note that the protoconchifer already shows a decision into a head-foot and a visceral sac. The latter is covered by a low conical shell, the former has already differentiated muscular appendages. There is not a simple creeping sole. In the protocephalopod, note the incipient chamber formation, the formation of a funnel complex from heterogeneous elements, the positional relationships of the arm bases (covering the head, marked by dotted surface) to the funnel, mouth and sense organs!

The “*visceral sac*” must be imagined in the form suggested by Textfigure 134 b, with a bluntly cone-shaped outer shell, the hypostracum of which was differentiated to form typical *chambers*. The posteriorly broadened roof of the mantle cavity with the anus represents the morphological hind-end and still exhibits traces of ancient segmentation in the form of at least two distinct metamereres. These are repeated organ complexes arranged around the two pairs of gills; to each of these coelomducts, renal sacs, vessels and their derivatives are associated in perfectly corresponding fashion.

The mantle slit is subsequently taken up by the “*funnel apparatus*”; it is composed of the two lateral, apparently most ancient parts forming the funnel pouches, to

310 which the funnel tube is added posteriorly, the “*nuchal attachment*” anteriorly. The structure separating the funnel tube from the funnel pouches, i.e. the “*funnel septum*”, extends posteriorly as a muscular ridge called the “*funnel retractor*” reaching to the deep part of the lateral mantle cavity.

The peculiarity of the *dibranchiate* type, so far as it is expressed at embryonic stages, can be visualized by a comparison between Textfigures 134 b and 136: the “*primary shell epithelium*” does not form a distinct invagination of the shell gland as observed in other conchifers (Textfig. 13) and surmised in *Nautilus* (Vol. 1, p. 57). This shell epithelium is already spread in its definitive form (Textfig. 135 a); it becomes covered by a “*shell fold*”, so an epithelial “*shell sac*” is formed in which the shell will be secreted. It is, in principle, conceivable that in an ancestor the earliest shell rudiment was formed *prior* to complete closure of the shell sac, in a way suggested by (the deliberately schematic) Textfigure 135. But in no case does that occur in a recent type.



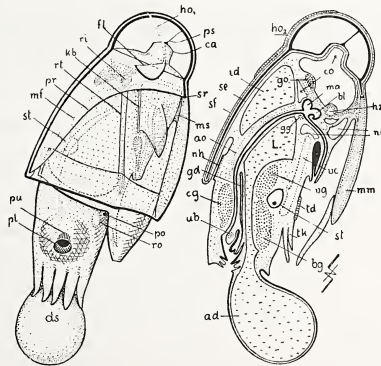
Textfigure 135. — The development of the shell, shell fold, shell sac, mantle cavity and muscular mantle in their natural correlation; illustrated by schematic medial sections (cf. Textfigs. 42 and 50) of embryos of an ideal (archetypal) dibranchiate. This can be compared with the archetypal condition of a conchifer (Textfigs. 13 and 134). More detailed explanations with Textfigures 43. x, y: anterior and posterior rim of growing shell; sf: shell fold; om: ostracal matrix generating the marginal growth of the shell; ms: mesenchyme of the soft mantle rim representing the rudiment of the muscular mantle (mm); ma: mantle rim; mh: mantle cavity; pm: posterior part of the membranous (primary) mantle; n: scar of shell sac closure (ss); se: secondary shell epithelium; sr: lateral edge of shell.

The posterior part of the dibranchiate shell (“*phragmocone*”) shows the typical chamber formation, at least in the older forms, whereas the wall of the living chamber remains rudimentary from the outset, at the most forming a “*proostracum*” from the dorsal part. To the outside a special sheath layer is added, the “*periostracum*”, while the retreating shell rim is progressively replaced by the massive, fleshy plate forming the “*muscular mantle*” (Textfig. 135 b); the latter develops at the expense of the typical membranous mantle of molluscs, which is conserved in some rudiments only. It is the muscular mantle that forms most of “*mantle sac*”; it shows a tendency both in

311 systematic series (i.e. phylogenetically) and individually (i.e. ontogenetically) to expand progressively at the expense of the *shell* (or the shell sac, or the gap representing it at an early stage) whose *development is retarded* and eventually ends in degeneration.

The number of rudiments forming "*prehensile arms*" is reduced to a maximum of 10, and to a maximum of 8 for the "*buccal arms*"; this reduction is related to a much more slender body shape, which builds on a more complex architecture. The arms produce true *suckers*, the rudiments of which are transverse papillae in single file (Textfig. 51). The arm pillars which embrace the head become fused to form continuous "*head covers*"; their edges next to the eye, which are termed "*ocular edges*", become connected with one another via a fold arising from the primary head skin ("posterior connecting piece"). Together with the latter, they form a protective envelope for the eye ball, the rim being contracted in the course of embryonic and larval development to form the "*primary lid*". Where the primary pupil has disappeared in closing the eye chamber, an *eye lens* is formed, and surrounding it on the outside an *iris* fold arises and delimits the secondary pupil.

The "*funnel lobes*", which are the rudiments of the funnel tube, becomes fused by a *seam* in the ventral midline; thus a solid, funnel-shaped tube is formed (Pl. 4). In the



Textfigure 136. — Ideal prototype of an advanced dibranchiate embryo (for special explanations see Textfig. 55). As a developmental stage, this is not homologous (for most parts) to the stage represented in Textfigure 134 (See also Textfig. 137).

- 312 area of the mantle cavity roof, only the *posterior* (lower) *pair of gills* of *Nautilus* is formed (Textfigs. 90, 91), whereas of the anterior metamer of *Nautilus* only the gonoduct issues are conserved.

Only a future study of *Nautilus* ontogenesis will tell us how far the Plates 1 and 24 are specific for the early development of dibranchiates (See also Textfigs. 31 and 33).

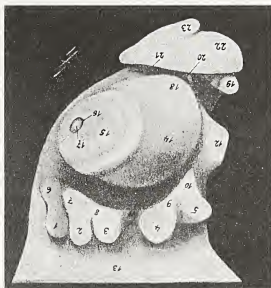
The main subject of Volume I was the *modification of the dibranchiate type* considering the postembryonic stages, i.e. those more advanced developmental stages exposed to direct struggle for existence. Their study led to a general revision of *systematics* based on both comparative anatomy and embryonic development, although the latter was given only cursory treatment.

Since for Cephalopoda in general a much higher number of arms is typical (Cf. Vol. I, pp. 62, 64), one cannot characterize the *Decapoda* solely by their arm number (10) within the dibranchiates. Forms that were already octopod-like may well have had as many arms! More surprising is the observation that (in contrast to my earlier assumption: Vol. I, pp. 110, 115) the sharp differentiation of *tentacular arms* is neither a diagnostic nor a *typical feature of decapods*. As far as we know (Naef, 1922, pp. 25, 167 and 252), the *belemnoids* did not yet have this differentiation, and in the development of the recent groups we have seen stages (Pls. 15, 23) that suggest an *originally homomorphic differentiation of all 10 arms*. The Sepioidea and Teuthoidea, along with their belemnoid protostages (not yet identified), thus can be considered a special group of relatives, which was not given a name of its own (Vol. I, p. 791). To avoid nomenclatural complications, I here propose the designation "Tentaculifera" for this group.

Absolutely positive, generalized and exclusive *decapod characters* appear to be provided by the structure of the *suckers* (Vol. I, p. 662). Otherwise any dibranchiate cephalopod *not specialized as an octopod* can be considered a decapod, so their diagnose reads: dibranchiates in which 10 prehensile arms and generally 8 buccal arm rudiments are formed,—in which the wall of the suction chamber of suckers produces a strong, cuticular "*horny ring*" (made of "keratohitin") with denticles on its free edge, able to transform into a hook,—in which the normal suckers are separated from their muscular "*carrier*" or "*basal pad*" by a deep constriction, so that a thin "*stalk*" remains as the only connection to the base.

- 313 The more special diagnose for the *Tentaculifera* then reads:

Decapods in which the fourth arm pair is transformed into tentacular arms by lengthening of the basal part, devoid of suckers, into a “*tentacular stalk*”, more or less marked broadening of the distal part into a “*tentacular club*”, and sinking of the stalk bases behind the ventral arms in “*tentacular pouches*”,—in which the rudiments of the *renal pores* move away from the gill base and approach the anus,—in which the funnel tube forms a valve, (except in cranchiids)—in which the funnel attachments are well developed and persist (except in cranchiids).



Textfigure 137. — Typical decapod embryo at stage XI (for detailed explanations see Textfig. 44). — Here the embryo is shown in the morphological orientation, like Textfigure 134, i.e. head-foot down, visceral sac up. Note the arrangement of the arms in 3 dorsal (1-3) and 2 ventral (4, 5) arm pairs, and the basal arm parts (6-10) positioned around the eye and its stalk (14). — 12: funnel tube; 19: gill.

For the systematic arrangement of this group see Volume 1, page 791 (C) and Textfigure 59. The “*Diploconidae*”, which are now called *Diplobelidae* Naef (1927), still might turn out as a *belemnoid variant* of the *Tentaculifera*. This conjecture is simply based on the observation that the structure of other belemnoids excludes a close relationship with the *Sepioidea*, whereas the latter clearly must be derived from a belemnoid type.

In contrast to the decapods, the *octopods* are marked by a long series of secondary modifications separating them from the primary type of the *dibranchiates*, in combination with some *primary* features suppressed by the decapods or at least by their extant representatives (Cf. Vol. 1, p. 655). Such primary features are represented by the purely *muscular suckers* (Vol. 1, p. 662) and by the close positional relation of the *renal pores* to the base of the gills in an archetypal fashion (Vol. 1, pp. 663, 664). The

absence of a special differentiation of tentacular arms is not a strict diagnostic feature, in contrast to the *lack* of a homolog to the decapodan *mediodorsal arms*, and to the lack of a *primary mediodorsal* part of the *mantle cavity* and of a *nuchal attachment*.

Further negative features are: the complete lack of a *buccal arm crown* and of a *funnel valve*, and especially of a *proostracum* in the shell and of a concave cone structure, not to mention the lacking chamber formation (p. 276).



Textfigure 138. — Advanced octopod embryo (See Textfig. 46 for further explanations). — Note especially that only two dorsal arm pairs (1, 2) are present. Cf. Textfigures 136, 137. Note also enveloping of the head by the head covers (11, 12, 13), which turn their ocular edge to the eye mass in preparation of the primary lid formation.

The *positive*, constructive elements in turn are: the strong predominance of the *muscular mantle* and of the musculature in general. The octopods are markedly *muscular animals!* The peculiar differentiation of a *secondary mediodorsal mantle cavity* is related to the replacement of the proostracum by muscular mantle structures (Cf. Vol. 1, p. 654); this secondary mantle cavity is derived from *primary laterodorsal* slits that extend posteriorly around the stellate ganglia and stellar nerves and join medially with one another; they first remain independent from the lateroventral mantle cavity when extending to the posterior part of the mantle sac (p. 260, Textfig. 116).— Similar positive features are the general modifications of the gill (Vol. 1, p. 665) which are related to the transformed pattern of gill vessels, the formation of the *longitudinal canal* in the gill (Vol. 1, p. 665), and the formation of an *Adductor pallii medianus* from the anterior edge of the anteriorly shifted septum of the ventral mantle cavity.

The further transformation of the dibranchiate type is again considered in the framework of a *systematic survey of the families*. Those with numbers in parentheses 315 are the families for which embryological data are now available. These numbers refer to the next following list of Mediterranean cephalopods, in which the data are specified in greater detail (pp. 334-335).

A systematic overview of the families of dibranchiate cephalopods

(Cf. Vol. 1, p. 808)

1st Order: Decapoda

- 1st Suborder: Belemnoidea +. Aulacoceratidae, Xiphoteuthidae, Phragmoteuthidae, Belemnitidae, Diplobelidae, Vasseuriidae.
- 2nd Suborder: Teuthoidea.
- a) Prototeuthoidea +: Plesioteuthidae, Leptoteuthidae, Geoteuthidae, Belopeltidae, Lioteuthidae
- b) Mesoteuthoidea +: Trachyteuthidae, Beloteuthidae, Palaeololiginidae, Celaenidae.
- c) Metateuthoidea myopsida: Loliginidae (1-4), Promachoteuthidae, Lepidoteuthidae.
- d) Metateuthoidea oegopsida: Ctenopterygidae (nova familia), Bathyteuthidae (5), Gonatidae (10), Enoploteuthidae (6-9), Onychoteuthidae (14), Histioteuthidae (15-16), Alluroteuthidae, Brachyteuthidae (17), Chiroteuthidae (18), Cranchiidae (19-21), Joubiniteuthidae, Architeuthidae, Psychroteuthidae, Ommatostrephidae (22-25), Thysanoteuthidae (26).
- 3rd Suborder: Sepioidea. Belemnosidae +. Belopteridae +; Spirulirostridae +, Spirulirostrinidae +, Spirulidae (30), Sepiidae (27-29), Sepiolidae (31-43).

2nd Order: Octopoda

- 1st Suborder: Palaeoctopoda +. Palaeoctopodidae.
- 2nd Suborder: Cirroteuthoidea. Vampyroteuthidae, Cirroteuthidae. Opisthoteuthidae.
- 3rd Suborder: Polypodoidea.
- a) Ctenoglossa: Amphitretidae, Bolitaenidae.
- b) Heteroglossa: Octopodidae (44-51), Argonautidae (52-54).

316 **A list of Mediterranean cephalopod species, with indications of the available developmental data**

The complete names of the 54 species of dibranchiates recorded in the Bay of Naples and near Messina are combined here with data (given as symbols) on their development. They indicate that I have obtained, either from my own observations or from trustworthy literature, the following data:

S: the spermatophores, O: the mature ovarian eggs, E: the spawned eggs and at least a few embryonic stages, L: the larvae (where they exist), J: advanced juvenile stages that are more or less clearly distinct from the adult stage, A: the adult stage irrespective of complete sexual maturity or definitive size, X: no larval stage in the ontogenesis, ?: undistinguishable objects. The species #20 and #21 are not securely established (Cf. Vol. 1, pp. 405, 409). In the Mediterranean, *Spirula* is represented only by its drifted shells (Vol. 1, p. 505).

1. <i>Loligo vulgaris</i> Lam. 1799.	S	O	E	L	J	A
2. <i>Loligo forbesi</i> Steenstr. 1856	S	-	E	L	J	A
3. <i>Alloteuthis media</i> (L. 1767) Naef MS, Wülker 1920.	S	O	E	L	J	A
4. <i>Alloteuthis subulata</i> (Lam 1799) Naef 1921	S	O	E	L	J	A
5. <i>Ctenopteryx siculus</i> (Vér. 1851) Pfeff. 1900	-	-	-	L	J	A
6. <i>Pyroteuthis margaritifera</i> (Rüppell 1844) Hoyle 1904	S	O	?	L	J	A
7. <i>Abralia veranyi</i> (Rüpp. 1884) Pfeff. 1912	S	O	-	L	J	A
8. <i>Abraliopsis morrissi</i> (Vér. 1837) Pfeff. 1900	S	-	-	L	J	A
9. <i>Thelidoteuthis alessandrinii</i> (Vérany 1851) Chun 1910	-	-	-	L	J	A
10. <i>Gonatus fabricii</i> (Licht. 1818) Steenstr. 1880	-	-	-	L	J	A
11. <i>Onychoteuthis banksi</i> (Leach 1817) Fér. & d'Orb. 1839	-	-	-	L	J	A
12. <i>Chaunoteuthis mollis</i> Appellöf 1891	S	-	-	?	J	A
13. <i>Ancistroteuthis lichtensteini</i> (d'Orb. 1839) Gray 1849	-	-	-	L	J	A
14. <i>Octopodoteuthis sicula</i> Rüpp. 1844	-	-	-	L	J	A
15. <i>Calliteuthis reversa</i> Verr. 1880	-	-	?	L	J	A
16. <i>Histioteuthis bonelliana</i> (Fér. 1835) d'Orb. 1839	-	-	?	L	J	A
17. <i>Brachiotheuthis riisei</i> (Steenstr. 1882) Chun 1910	-	-	-	L	J	A
18. <i>Chirotheuthis veranyi</i> (Fér. 1835) d'Orb. 1839	-	-	-	L	J	A
19. <i>Galiteuthis armata</i> Joubin 1898	-	-	-	L	J	A
20. <i>Leachia cyclura</i> Lesueur 1821	-	-	-	L	J	A
21. <i>Liocranchia reinhardti</i> (Steenstrup 1856) Pfeff. 1884	-	-	-	L	J	A
22. <i>Illex coindetii</i> (Vér. 1837) Steenstr. 1880	S	O	-	?	J	A
23. <i>Todaropsis eblanae</i> (Ball 1841) Posselt 1893	S	-	-	?	J	A

	24. <i>Ommatostrephes sagittatus</i> (Lam. 1799) d'Orb. 1848	-	-	?	L	J	A
317	25. <i>Sthenoteuthis bartrami</i> (Lesueur 1821) Verr. 1880	-	-	?	L	J	A
	26. <i>Thysanoteuthis rhombus</i> Troschel 1857	-	-	?	L	J	A
	27. <i>Sepia officinalis</i> L. 1758	S	O	E	X	J	A
	28. <i>Sepia orbignyana</i> Fér. 1826	S	O	E	X	J	A
	29. <i>Sepia elegans</i> d'Orb. 1839	S	O	E	X	J	A
	30. <i>Spirula spirula</i> (L. 1767) Hoyle 1909	-	O	-	X	J	A
	31. <i>Rossia macrosoma</i> (Delle Chiaje 1829) d'Orb. 1839	-	O	E	X	J	A
	32. <i>Heteroteuthis dispar</i> (Rüpp. 1845) Gray 1849	S	O	-	X	J	A
	33. <i>Sepiola steenstrupiana</i> Levy 1912	S	O	?	X	?	A
	34. <i>Sepiola aurantiaca</i> Jatta 1896	S	O	?	X	?	A
	35. <i>Sepiola ligulata</i> Naef 1912	S	O	?	X	?	A
	36. <i>Sepiola rondeleti</i> Steenstr. 1856	S	O	?	X	?	A
	37. <i>Sepiola affinis</i> Naef 1912	S	O	?	X	?	A
	38. <i>Sepiola intermedia</i> Naef 1912	S	O	?	X	?	A
	39. <i>Sepiola robusta</i> Naef 1912	S	O	?	X	?	A
	40. <i>Rondeletiola minor</i> (Naef 1912) 1921	S	O	E	X	J	A
	41. <i>Sepietta oweniana</i> (Pfeff. 1908) Naef 1912	S	O	E	X	J	A
	42. <i>Sepietta obscura</i> Naef 1916	S	O	E	X	J	A
	43. <i>Sepietta neglecta</i> Naef 1916	S	O	?	X	?	A
	44. <i>Octopus vulgaris</i> Lam. 1799	S	O	E	L	J	A
	45. <i>Octopus saluzzii</i> Vérany 1837	S	O	-	?	J	A
	46. <i>Octopus macropus</i> Risso 1826	S	O	-	L	J	A
	47. <i>Octopus defilippii</i> Vérany 1851	S	O	E	?	J	A
	48. <i>Octopus tetracirrus</i> Delle Chiaje 1829	S	O	-	?	J	A
	49. <i>Octopus unircirrus</i> (Delle Chiaje MS) d'Orb. 1838	S	O	-	?	J	A
	50. <i>Eledone moschata</i> (Lam. 1799) Leach 1817	S	O	E	X	J	A
	51. <i>Eledone cirrosa</i> (Lam. 1799) Fér. & d'Orb. 1838	S	O	-	X	J	A
	52. <i>Tremoctopus violaceus</i> Delle Chiaje 1829	S	O	E	L	J	A
	53. <i>Ocythoë tuberculata</i> Rafinesque 1814	S	O	E	L	J	A
	54. <i>Argonauta argo</i> L. 1758	S	O	E	L	J	A

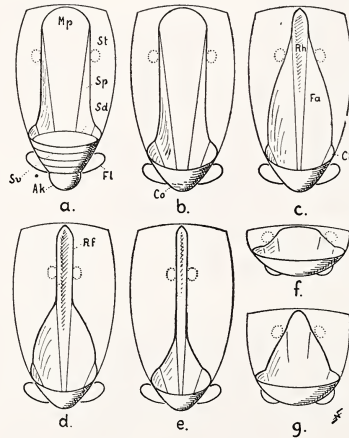
Part of my material was already studied by G. Jatta, whose work originally I should have continued (Cf. Vol. 1, pp. v-ix). With regard to his preliminary indications, a few corrections should be recalled: the eggs figured in Jatta's Plate 2, Figure 4 cannot be identified; they certainly belong to *Sepiola*, but surely not to *S. rondeleti*; likewise the eggs figured in his Plate 7, Figure 7. The eggs figured in Plate 2, Figure 7 are those of *S. elegans*, not *S. orbignyana*; likewise those in Plate 7, Figure 17. Conversely, those in Plate 8, Figures 7 and 8 are eggs of *S. orbignyana*, not *S. elegans*

(See also Vol. 1, p. ix on eggs and newly identified juvenile forms).

One will easily realise that the present results are by no means complete, not even in the frame defined in the Preface. We have gained only fragmentary knowledge about the embryology of the Mediterranean cephalopods. Especially, a comprehensive insight into oegopsid development has remained a vain wish. Even more important would have been the recovery of embryonic stages of *Spirula* (p. 208), or of *Idiosepius*, because they could provide considerable systematic-morphological and phylogenetic clarification (p. 211).

Nevertheless, a considerable improvement of our knowledge about the morphological diversity of cephalopods is the result, even in comparison to Volume 1, and we have to rest content with it. In the following lines, I briefly formulate the characteristic peculiarities of the greater subgroups as far as they appear in the embryo:

Of the embryonic development of the *belemnoids*, we can obtain *direct* evidence only from fossil shell nuclei. This is visualized in Textfigure 136, the features of preliminary stages being suggested by Textfigure 135 b. We can furthermore assume in

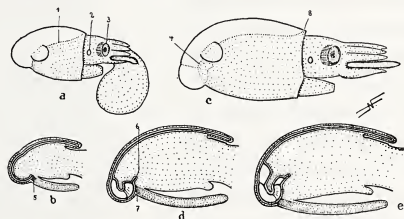


Textfigure 139. — Figure illustrating the modification of the belemnoid type in teuthoids, with total inhibition of the phragmocone formation and partial inhibition of proostracal growth (See further explanations in Textfig. 60). a: belemnoid; b: prototeuthoid; c: mesoteuthoid; d: metateuthoid; e: extreme degeneration of the proostracum; f, g: early embryonic stages.

theory that the archetypal course of dibranchiate development (pp. 89-149) was embodied in at least the earliest belemnoids.

The *teuthoids* are characterized by an almost complete suppression of phragmocone formation at the early preliminary stages (Textfig. 135 b), with subsequent, variably marked, degeneration of the cone rudiment (Textfig. 63) and of the proostracum (Textfig. 139). The relative predominance of the muscular mantle is partly achieved stepwise, with a gross succession of prototeuthoid, mesoteuthoid and metateuthoid conditions, in some instances followed by further reductions.

In myopsid teuthoids the cone is totally rudimentary from the outset, as far as we know (*Lepidoteuthis* ? *Promachoteuthis* ?), although the ontogenetic pattern is otherwise almost perfectly archetypal. In contrast, *oegopsids* show a complete formation of the *posterior shell rudiment*, but within a strongly modified pattern of embryonic stages. We have been able to explain its general features by assuming a *secondary reduction of the yoliness*, hence of the size of the eggs; this results, as part of an adaptation to a *nekto-pelagic mode of life*, in a *shortening of embryonic development*, with acceleration of some vital organs and retardation of others. The number of "larvae" thus produced is extremely high in comparison to the norm. *Acceleration of*



Textfigure 140. — Typical development of sepipoids. From Volume 1, page 491. Advanced embryonic stages and their medial sections. See for comparison Textfigures 135 and 136 to assess the basically dibranchian (decapod) condition, but with an increasing curvature of the proostracum and a resulting ventral rotation of the initial chamber. The ventral edge of the shell is pushed into the soft body; the muscular mantle thus comes to insert on its outside. These effects are subsequently exaggerated (d, e) as a function of increasing ventral curvature of the phragmocone. To construct the definitive condition, we must admit an ontogenetic shift similar to the systematic (phylogenetic) derivation (Textfig. 86).

1: edge of the proostracum; 2: olfactory tubercle; 3: primary eye lid; 4: mantle insertion on the outer surface of the phragmocone; 5: same on ventral shell rim; 6: ventral edge of the shell, penetrating into the soft body; 7: shifted mantle insertion; 8: anterior edge of muscular mantle.

The ventral curvature is strongly pronounced, similar to what is seen in *Spirulirostra*; it must have been weaker in the archetypal condition. The muscular mantle is shown contracted; in the expanded condition the body would appear almost globular.

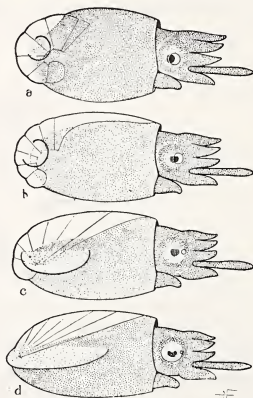
attainment of a functional state in oegopsids concerns the nerve centers, the eyes, one basal sucker on each arm and a few basal club suckers on the tentacles, the funnel and the mantle sac. Retarded structures are the distal arm parts, the whole third and fifth arm pairs, the gills, kidneys and many small vessels. The outer yolk sac remains totally rudimentary.

319 For the *sepioids*, the conditions of the embryonic *shell* in relation to the *mantle sac* are also characteristic. For the fossil types (Belemnosidae, Belopteridae, Spirulirostridae), a close similarity to the archetypal conditions given in Textfigure 140 can be reconstructed from the shell nuclei, and *Spirula* (Textfig. 86 b) appears still very close to them. Perhaps the same is true for *Idiosepius*.—In contrast, the embryologically known forms of sepiids and sepiolids can be derived only indirectly from this remote norm, via fossil intermediates (Spirulirostrinidae, Belosepiinae) as far as the sepiids are concerned:

In the *sepiids* the proostracum is almost completely suppressed from the outset (Textfig. 88); the septa are very slanting and the chambers flattened (Textfig. 141 c, d). Even the ventral rim of the shell (Textfig. 94 b) reveals the sepioid insertion of the shell in the muscular mantle only vaguely.—Conversely, in the *sepiolids* it is the proostracum, or at least the corresponding part of the shell sac, that is conserved for a longer time; the phragmocone part of the shell sac in turn degenerates completely during embryonic development (Textfig. 100). Its originally sepioid nature is expressed, however, in its general form that is recognizable in *all representatives* (more on that later!).

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Among the *octopods*, the development of the *cirroteuthoids* unfortunately remains unknown. All we know is that *Opisthoteuthis* (see Meyer, 1906) produces relatively few, large ovarian eggs, hence lacks a larval phase like in *Octopus* or



Textfigure 141. — Juvenile stages of sepioids. a) *Spirula*. b) *Spirulirostra* (somewhat too strongly curved!); c) *Belosepia* (somewhat too highly vaulted; imagine the shell axially more compressed). d) *Sepia*. (cf. Textfig. 85).

Argonauta; the hatchlings must be advanced juvenile stages of generally normal octopodan aspect (Textfig. 116 a). The *polypodoids* are very different in this respect: a common feature of the Heteroglossa, which comprise the specially related octopodids (small egg forms) and argonautids, is the small size of the eggs and larvae as in *Octopus* (Textfigs. 116-120), and it is likely that this is the primary condition. A further indication is the generalized occurrence of a special larval organ, namely the setal tufts in the skin (Textfig. 122), which supposedly occurs in cirroteuthoids as well.

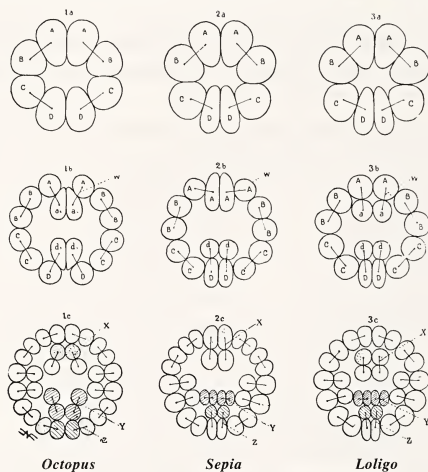
The special character of the *polypodoids* would then be the advanced *degeneration of the shell*, the history of which can be read from embryonic development (stages A-D):

321 The rudiment is a strikingly small, roundish shell sac reminiscent of a condition suggested by Textfigure 116 b (stage A). This rudiment is subsequently compressed both from the anterior and posterior ends so that a small transverse sac results; in direct continuation this would lead to a clasp situated in the posterior part of the mantle, situated slightly dorsally (stage B). But this sac in fact splits in two, each of the paired lateral tubes directing its function to the formation of a rod-shaped shell relic (stage C). While the latter are really formed in octopodids, the shell sac rudiments disintegrate in *Argonauta argo* and probably also in the other argonautids (I have not been able to verify it in all the forms), and from the beginning they are more delicate than in octopodids (stage D). Stages A-D are typical for the four systematic (phylogenetic) grades: A) Octopoda, B) Polypodoidea, C) Heteroglossa, D) Argonautidae. This gradation cannot be really demonstrated, nor refuted, in all details. Without forming a phylogenetic or merely morphological series, the following genera nevertheless represent the four stages: A) *Vampyroteuthis* ("*Watasella*", Sasaki 1920), B) *Stauroteuthis* (ibid.), C) *Octopus* (cf. Vol. 1, p. 664), D) *Argonauta*.

A surprising observation in this comparative study are the different aspects of the early *cleavage patterns*. Textfigure 143 shows the three types studied in detail, with a suggested nomenclature that should be useful to future comparative analyses.

Especially noteworthy are the following differences, which appear already in the second line (16 cells): whereas in *Octopus* A and D produce almost identical micromeres (a and d), in *Loligo* these derivations are different, in relation to the size difference between A and D. But all four micromeres end up inside the circle of macromeres. The same is true for D of *Sepia*, but not for A, which cleaves in such a way that two macromeres result from each. From the medial ones micromeres are

derived at the 32 cell stage (Textfigure 142, 2 c), so that a pattern obtains which is similar to *Loligo*, to which this stage is similar also in all other aspects. However, an element (marked as dotted) remains in the peripheral ring, whereas in *Octopus* it lies inside the ring much like in *Loligo*. *Octopus* in turn differs from both decapods with respect to the D octant: 2 D produces no new micromeres, but cleaves radially, so that two macromeres are formed. The medial one (marked by oblique hatching) would thus have a different homology in terms of its *origin* and in terms of its *fate* (Cf. p. 21). Although the latter cannot be determined with certainty, one may say that in octopods this cell will contribute to the definitive blastoderm rim, hence to the yolk epithelium,



Textfigure 142. — Schematic, comparative representation of typical cleavage processes in *Octopus vulgaris*, *Sepia officinalis* and *Loligo vulgaris*. The upper row shows the 8-cell stages with the respective positions of the last mitotic spindles; the middle row shows the 16-cell stages with corresponding specifications, the bottom row the 32-cell stages (cf. Pls. 24, 13 and 1). A designation of blastomeres is tentatively given; it has to be symmetrical, starting out from the 8-cell stage. The latter can be compared roughly to the 4-cell stage of other molluscs, if the two octomeres D are considered as equal to the single tetramer D of Textfigure 7.

The daughter cell should be distinguished in such a way that micromeres (i.e. the cells coming to lie within the blastoderm) are given lower case letters, as is usual, counting the cleavage steps from the 8-cell stage and adding a corresponding numeral to the letter (1 D, 1 d). The position of the cells could then be specified by symbols added after the letter (allowing one to distinguish medial, lateral, anterior and posterior), e.g. using Greek letters.

presumably also to the gut rudiment, whereas in decapods it will not, entailing necessarily the consideration given here (p. 21).

2. On Disturbed and Abnormal Morphogenesis and Its Relation to Normal Development

Contents: a. The regeneration of outer organs (p. 343). b. On abnormal development of uninjured and undisturbed parts (p. 347). c. On experimental generation of abnormal morphogenesis (p. 348).

This volume has so far dealt with developmental processes observed under normal, nearly natural conditions of development in undisturbed embryogenesis. The descriptions were made from a biological viewpoint (p. 5), considering that highly significant and problematic *achievements* of the organism are observed here, and that their comparative study is a means of understanding the general interrelationships underlying its existence and action. It is obvious that we do not really know a person we have observed only under every day conditions, and, likewise, animal morphogenesis is not thoroughly understood from considering only its rather rigid norm, which is regularly expressed in the absence of any disturbing factor. A deliberate limitation of this sort would carry the danger of overlooking possibilities to gain insight into the flexibility, variability and augmentability of formations. Although the main subject of this monograph remains the systematic study of the typical (normal), we will not refrain from having a look across the fence and report observations that might be welcome to other parties. I am indeed firmly convinced that the present hiatus between comparative and experimental morphology is obstructive and absurd for both sides, that a close relation between them is desirable instead; it has therefore been considered an accessory aim of this work (See the Preface) to prepare the ground for a dynamic analysis of the material compared here by a systematic study. A glimpse of the recent literature indeed reveals the frequent lack of a sound knowledge of the experimental objects and their relation to the greater natural context. We can only

hope to grasp and dissect the functioning and interaction of factors if we know the animal studied or developmental stage in all its details and recognize its multiple relationships with other members of the greater framework of order.

In transgressing its limits, we cannot of course indulge in the same fullness of detail and forcefulness of description as in our own field, so we often have to content ourselves with some hints.

a. The Regeneration of the Outer Organs

When scanning through a large sample of various cephalopods, one will always come across specimens that show traces of some healed injuries. Skin lesions of all sorts appear to close quickly, although in captivity they often cause illness and early death. Even replacement of larger parts of the body appears to occur often under natural conditions; thus suckers lost accidentally (i.e. not as part of a normal developmental course, which frequently is the case) are replaced; therefore one often finds small, developing suckers in positions where normally fully developed ones are observed. Such occurrences may generate difficulties for descriptions, especially in species where sucker size differences are typical distinctive features. In young animals of all species, lost suckers are probably replaced regularly. The arms (including decapod tentacles) regenerate as well, as can be seen from the occurrence of suddenly tapering arm ends on a stump of normal proportions. The regenerated parts closely follow the normal pattern of differentiation, e.g. in terms of the arrangement and rearrangement of suckers. The capacity of *Octopus vulgaris* to regenerate arms was known already to Aristotle and Plinius. I have furthermore seen obviously regenerated arm tips in *Sepia officinalis*, *Sepietta obscura*, *Loligo vulgaris*, *Illex coindetii*, *Octopus macropus*, *O. defilippii* and *O. saluzzii*, *Eledone moschata* and *E. cirrosa*, *Octopus tetracirrus* and *O. unicolor*, *Argonauta argo*, *Ocythoë tuberculata*. I have observed many times the regeneration process in captive individuals of *Sepia officinalis* and *Octopus vulgaris*. In healthy individual of *Octopus vulgaris* kept under good aquarium conditions, arm tips were cut off several times to let them regenerate successively; even whole arms are fully regenerated under aquarium conditions, at least in young animals.

After amputation of an arm tip (about $\frac{1}{10}$ to $\frac{1}{6}$ of the arm) the wound contracts rapidly, without much bleeding; it is tightly closed after 1-2 days. The last conserved sucker takes up a terminal position. On the third or fourth day a regenerating bud appears at the site of the scar, which faces outwards. It rapidly grows to become a tail-like appendage with transverse ridges instead of suckers (after 1 week). They subsequently become concentrated in the form of uniserial papillae devoid of a suction chamber, as in normal development (Textfig. 51). Subsequently, they are arranged in a zig-zag pattern; this whole development progresses from the proximal to the distal zone of the regenerating part. Only the first few rudiments are somewhat exceptional in that they grow particularly fast, keep a greater distance from one another and thus form a transitional pattern at the base of the regenerating part, close to the stump (Cf. Vol. 1, Pl. 9).

At the end of the third week, the regenerating part has the aspect of a normal, though somewhat too thin arm end; in *Octopus vulgaris* and other octopodids it subsequently grows to a normal size perfectly corresponding to the size of the stump. Depending on the extent of the original injury, some irregularities may persist for longer times, altering the arm proportions so that the identification of freshly captured individuals may become difficult. (Remember that the relative length and thickness of arms are among the best species-specific characters in this family; see also Vol. 1).

In some species injuries of the arms appear to occur particularly frequently, or else to heal and regenerate more slowly than in others. Thus one never finds a completely or at least nearly intact specimen of *Octopus (Scaevurgus) tetracirrus*. The same is true for *O. defilippii*, which is known to autotomize its arms. The lost arms, which are released by rapid muscle contractions, survive for some time and continue to exhibit the same mobility and excitability as the arms that have remained intact. They are regenerated completely by the animal. The broodshell arms of *Argonauta* show an interesting behavior: I have seen a very incompletely regenerated dorsal arm in a female individual; the intact dorsal arm partly took over the function of the lost parts and assisted in the building of the other side, though insufficiently, so that the shell became asymmetrical. (Grimpe reported on this, i.e. my observation, already in Brehm's Tierleben, Vol. 1, 1918)

See also Lange (1920) on the processes involved in the regeneration of octopod arms; part of her work was done under my supervision.

The regeneration of the arms and tentacular arms in decapods in general takes the same course as in octopod arm regeneration. The suckers must of course be arranged

in 2-8 rows as in normal development. The regenerated arms thus show situations like those figured in Plate 21. I have followed the process in detail only in *Sepia officinalis*, but I have also been able to deduce its occurrence from observations on freshly caught specimens of *Sepietta oweniana* and *S. obscura*, *Loligo vulgaris*, *Alloteuthis media* and *Illex coindetii*. Particularly frequent injuries in the Naples area are due to a fishing gear named "Latero", used for catching especially *Sepia*, *Loligo* and *Illex*. One can deduce from these observations that the animals have been able to free themselves after capture. In these instances several (sometimes all) arms are injured near their base, i.e. in the section which was involved in seizing the bait, hence the barbed fishing tackle. In these animals the suckers and parts of the protective membranes are lacking or regenerating at the arm bases. Since several arms are similarly modified, one might easily misinterpret these modifications as malformations or even as normal peculiarities.

The regeneration of smaller parts of the fins, arm protective membranes, eye lids, mantle rim also can be observed on freshly caught specimens, and can be easily induced in captive individuals.

In general the regenerates express the same capacity for potencies of morphogenesis as the normal rudiments at the corresponding position. Occasionally the parts produced by regeneration are anomalous, however, e.g., regenerated tentacular clubs often have much lower numbers of suckers than normal ones; in the above-mentioned injuries due to a fishing tackle, the wound edge of the protective membranes healed in growing to fuse along the inner surface of the arm thus forming a tunnel (observed in *Illex* and in *Sepia orbignyana*).

The rather frequently *branched* arm tips are probably anomalous regenerates. I have no doubts about the possibility to obtain them experimentally; however, I had no time to do the necessary experiments. I have seen branched arms in *Octopus vulgaris*, *Eledone moschata* and *Sepietta obscura*. A similar interpretation imposes itself for the phenomenon of a small secondary fin on the main fin of *Sepia officinalis*, which I have seen once. The underlying principle seems to be a beginning regeneration in a half-severed part before the latter achieves a reintegration into the normal context.

Of special interest are *two examples of abnormal regeneration in the arm crown* of *Sepia officinalis*, which I intend to analyse elsewhere in detail. In both cases a deep injury had occurred that involved, directly or indirectly, the neighboring buccal lap-pets. The latter are understandable as buccal arm rudiments and can be compared to

the inner arm crown of *Nautilus* (Vol. 1, p. 178). It looks as if this characteristic could be more strongly expressed under anomalous conditions, i.e. whenever these rudiments were called upon to fulfill a special function after the loss of the neighboring arms;

In one individual (A), arms 2 and 3 and most of the tentacle of the left side had been lost, probably bitten off. The tentacle provides some evidence: the short, normal stump bears a typical, tapering regenerate. The second arm has produced only a very inconspicuous regenerate, which is connected to the first arm in the normal manner; arm 3 appears lost altogether. The neighboring third buccal lappet is abnormally well developed; it shows the normal connection with the other buccal lappets, but clearly shifted close to the position of the lacking third arm. It bears 4 rows of small suckers and is strongly muscular. So far for the surface aspect.

327 In the other individual (B) both dorsal arms appear to be missing lack altogether, probably also due to an injury. The dorsal buccal lappet has virtually taken up their position without losing its connection with the other buccal lappets; it looks like a rather weak arm. It is connected to the second arm of each side by a muscular web fold, in other words it represents the two dorsal arms in this respect. Its inner surface shows a hybrid condition: the basal part is connected to the other buccal lappets and is wrinkled like them. Next comes a zigzag row of small suckers grading into two rows of larger suckers followed by two zigzag rows towards the tip. A regular arrangement in four rows is not achieved.

Originally I considered these arms as pure buccal lappets in both A and B, and I have interpreted my experimental results accordingly; I wish to return to this subject now. A closer inspection involving dissection of the inner parts leads to a different result: in these two individuals, an arm has been formed that represents both the *prehensile and the buccal arms*, having adopted also the basic interconnections. In B it represents the dorsal buccal lappet as well as *the two dorsal arms*. In other words, *two buccal arm rudiments and two prehensile arms* have distally fused into one single, medial formation; the latter shows the structure of a normal arm (resting on two brachial roots) along with showing the connections with the other buccal lappets that are typical for the dorsal buccal lappet. This cannot be interpreted as a *simply* atavistic regeneration, but it could reflect a special effect of a normally existing tendency of this region to generate a fusion of arm rudiments (Cf. p. 225). In a similar way, in specimen A an arm has been formed that represents the third arm and the third buccal arm rudiment rather than the latter only.

The *question* about the *factor* inducing such fusions can probably be answered today: it lies in the generally strong *skin contraction* after injuries observed in cephalopods. Even large openings are thus rapidly closed so that the wounded tissue is inevitably concentrated in one point as it were. Since the fusion of arm rudiments is possible under normal conditions (p. 225), it must be strongly favored when several stumps are united by a common wound tissue from which new arm rudiments have to form.—Formations like in specimen B can be generated experimentally, but I have not been in a situation allowing me to wait for the formation of suckers.

Heavy injuries of the *shell* of *Sepia officinalis* can also be regenerated, as demonstrated occasionally by collected cuttlebones that are deformed. This does not of course represent a re-establishment of the primary structure; it is simply a superposition of shell material in a tentative approach to typical conditions. Somewhat more frequently one finds deformations that appear to be due to diseased shell epithelium (excrecences of various types).

b. On Abnormal Development of Intact and Undisturbed Specimens

Among the embryos of my cultures, I found rather frequently abnormal individuals; I have carefully sorted them out and collected them over a long time. Some recurrent phenomena are of special interest since they appear to obliterate the border lines between certain groups or developmental norms. The oegopsid-like stages are occasionally observed in normal egg masses of *Loligo vulgaris*; they resemble Figures 1-3 of Plate 10 in that the greater part of the yolk has been taken in by the embryo, which has not undergone the typical contraction normally leading to a constriction of the yolk sac. These and similar deformations arise particularly often when originally normal egg masses begin to show a high embryonic mortality. (Under our normal aquarium conditions it is rare that an egg mass undergoes the typical embryonic development from the beginning to the very end. See therefore below, section c).

I was particularly surprised to find an entire egg capsule of *Loligo vulgaris* containing embryos with inverted mantle rudiments, each of them looking like an umbrella turned inside out by a sudden gust (for the normal condition see Pl. 6, Figs. 1-9). Once the anomaly of growth had begun around stage X, it was irreversible of course.

It is probably due to an intrinsic cause; it is extremely rare that such a condition is caused by the excessively rapid escape movement triggered by a fixative, when the mantle of advanced embryos or larvae turns inside out.

During postembryonic development various deviations from the normal course of morphogenesis also can be observed. Of special interest are some cases of *double* hectocotylus differentiation in sepiolids; such cases are easily misinterpreted (by overhasty systematists) since the family contains species in which normally (as an expression of the respective archetype) both dorsal arms are equally modified (*Sepiolina nipponensis*, *Rossia*). I have seen double hectocotylyzation (cf. Appellöf, 1893) in one specimen of *Sepiola affinis*, *Sepietta oweniana* and *S. obscura*, respectively. A peculiar case also is a mature, otherwise normal male of *Alloteuthis media* with very large (though slightly abnormally structured) *nidamental glands*, but without accessory nidamental glands! The ostensible male gonad was not analyzed since the specimen (collected from a large catch) was too poorly preserved.

c. On Experimental Generation of Abnormal Morphogenesis

The aim of dynamic morphology, which is the counterpart of systematic morphology within the system of biological disciplines, first of all is the analysis of the texture made of stimulators and reactors, the common achievement of which is the ordered self-construction of the living organism (cf. Naef, 1923, Vierteljahrs. Naturf. Ges. Zürich). The harmony of potencies, which is taken for granted by systematic morphology, is here approached with experimental methods, and its phylogenetic modification is also taken into consideration.

Schimkewitsch (1899, 1900) described experiments he made to test the effect of various solutions on the embryonic development of *Loligo*. His results show that unnatural conditions not only kill cephalopod embryos, but that they can also generate malformations through partial damage (cf. Ranzi, 1926, 1928). Schimkewitsch considers these malformations as the result of chemical, osmotic and simple mechanical effects due to altered conditions of the surrounding medium. But apparently most of these malformations are due to deformation of dying parts and unequal inhibition of the course of development, partly also to atypical cell proliferation;

they would become scientifically interesting only if their *regularity* could be understood.

The observation that unfavorable conditions such as lack of oxygen or accumulation of carbon dioxide seem to cause malformations led me to an experimental approach guided by the idea that, in the case of slow and partial necrosis, the *regular suppression* of certain morphogenetic elements (be it nonappearance of certain *rudiments* or inhibition of certain *developmental steps*) should be obtained rather than necrotic deformation. This seems indeed possible.

I hope to be able to finish these experiments, which have been undertaken rather incidentally and without the necessary investment of technical means, time and intellectual efforts (See Foreword). The past few years have not permitted me to follow up this line, and I can therefore give here only a few indications and reflections:

I focussed my interest on *modifications of developmental conditions* within the *framework of phylogenetically conceivable* or (for certain forms) legitimately assumed conditions, excluding from my considerations any extreme and entirely unnatural condition. Since temperature variations within the limits of tolerance turned out to influence development only in terms of its time course, without altering the stage correlations of developing parts, there was not much latitude for experimental work: the main task was defining the effects of *modifications of the medium*.

From this point of view, some observations that were originally made under different aspects, appear interesting: the original aim was a study of the effects of (experimentally achieved) premature organ functioning. To this end, embryos of *Sepia* and *Sepiolo* were removed from their envelopes and raised in *sea water* (which was perfectly feasible). If very clean sea water is used, it is possible to keep early stages (from about stage X) for at least a few days in petri dishes (protected against dust, sun light and evaporation), and to raise embryos from stage XVI to the end of embryonic development. However, it is virtually impossible to avoid loss of the outer yolk sac around stages XVII and XIX; instead of resorbing this natural food reserve, the embryos generally drop the still sizable outer yolk sac; this results in a considerable weakening, which is perhaps counterbalanced by a certain protection against infections. In all events, the young animal thus gains full mobility.

If embryos of *Sepia officinalis* at stage XVII are carefully removed from their envelopes and transferred to clean sea water, preferably in dishes with a paraffin bottom in which circular depressions accommodate the yolk sacs (Cf. Pls. 18 and 19), one

will observe a very peculiar phenomenon: while the general development proceeds normally (especially careful treatment also avoiding an early loss of the outer yolk sac), the differentiation of the *primary lid* takes an aberrant route: it conserves and even enhances the normally transient function as a lid; it reacts to stimuli (touch, vibration, strong light) by contracting progressively fast, but not in a definitive contraction leading to the formation of a closed cornea, but only temporarily, in a reflex-like fashion. Morphological modifications following the embryonic stage attained inside the envelopes do occur, but they take the direct route of histological differentiation rather than an indirect one involving architectural complication.

Originally I thought this behavior was due to the premature functioning of the eye (although it is easy to observe that it is functional at even earlier stages inside the envelopes). It was a surprise to me when I found that the normal modification of the primary lid was *skipped even in total darkness*, i.e. when the petri dishes were covered by a double layer of black paper on a black table or in a drawer inside a darkroom. It is skipped also when the embryos remain in their chorion after removal of the outer gelatinous envelopes; the volume of the chorionic space then increases very strongly so that the embryo is virtually surrounded by sea water, without being otherwise exposed to a marked alteration of its living conditions.

331 The young cuttlefishes thus having an oegopsid or *Spirula* eye are perfectly viable and, with due care and some culture experience, can be raised to become fully valid animals. I have kept them, along with normal ones on moderately fine sand bottom for up to 3 or 4 months; they lived exactly like the other animals and easily captured *Mysis*. This feeding mode implies a perfect functioning of the eyes, which apparently is quite unimpaired: the young cuttlefish (Cf. Pl. 20, Fig. 2) carefully aim at their prey and shoot their tentacular arms, which are held tightly together, straight ahead—developing an astonishing *accuracy* of shooting.

An individual predisposition of this kind of *developmental inhibition* is highly unlikely. Repeated experiments indeed gave the same results in several cases. Unfortunately I was not able to pursue this study in a detailed analysis of the process, with ample material and sufficient technical means; I therefore consider my rights reserved for the future. Surely the results will depend on the age, i.e. the developmental stage of the embryos: somewhat more advanced embryos skipped the corneal closure as well, but they still formed a primary lid rudiment (similar to Figs. 1 and 2 of Pl. 5*) which I had overlooked when removing the embryos from their envelopes.

* Scientific Editor: the original text mentions "Figure 13 of Plate 5".

An any rate, the missing developmental step was otherwise not made up for subsequently, the *Spirula*-type eye (*with a functional primary lid*) remained so; thus a condition is conserved that must have existed in the ancestors of extant cuttlefish (Textfig. 136). The fact that this condition is still “potentially available”, i.e. retrievable, being expressed as a reaction to *appropriate stimuli* or to a lack of stimuli, is certainly meaningful in relation to the law of the conservative preliminary stages.

It is also useful to take the stimulating causes into consideration: they are probably related to a *modification of the medium* that closely approaches the environmental change occurring at normal hatching: whereas the primary lid closes completely in the intrachorionic fluid, it remains open in sea water! This occurs in a sepoid (perhaps in others too) having rather large eggs, a relatively long development and normally very complete juvenile equipment. We know that in the related *Spirula* which has markedly smaller eggs, the young of which hatch with 2 instead of 7 gas chambers in the shell (p. 210), the process artificially induced in *Sepia* occurs normally: inevitably *Spirula* hatches from the egg envelopes at a correspondingly underdeveloped stage of eye formation and finds itself in sea water much like my premature *Sepia*. Could this be interpreted as an omission of an archetypal step of sepoid development? Or was it, on the contrary, an addition of a factor related to an extended embryonic development in phylogenetically younger sepoid groups (p. 215) that triggered the ultimate modification of the protective apparatus of the eye?

There is no doubt about the following point: in the teuthoids there are also two distinct types, the myopsid and the oegopsid form. The *myopsid* (*Loligo*) type has a much longer embryonic development, whereas the *oegopsid* type has a doubtless secondarily shortened development (p. 337) leading to a juvenile form with variably incomplete ocular elements (p. 180). Unfortunately it is impossible to raise *Loligo* embryos with oegopsid lids outside their envelopes; these stages are in general very shortlived under artificial conditions. But it is of course absolutely conceivable that phylogenetic processes led to increasingly *premature hatching* with corresponding inhibition of the lid closure—something that may have happened in oegopsid squids as well as in *Spirula*.

Paleontological data also plead in favor of this idea: both the spirulids and the oegopsids are highly derived, *nektonic variants of an originally benthic type*; it was only in the final phase of writing Volume I that I became fully aware of this relationship. (For the teuthoids see above p. 152, for the sepoids see Vol. I, pp. 484 and 518, and above pp. 208-210).

Today I would draw the primary eye lids of both the archetypal sepioids (Vol. 1, p. 487) and teuthoids (Vol. 1, p. 136) strongly contracted in the adult stage, perhaps even that of the protodecapod (Vol. 1, p. 110). In contrast, in the protodibranchiates an open primary lid must have been the typical condition (Textfig. 28) given the very different modes of secondary closure in octopods and decapods.

It is obvious that the lid closure plays different roles in *nekto-pelagic* and in the *benthic* dibranchiates where it protects the orbital cavity from sediment particles. In purely optical terms the primary lid cannot have a major effect, surely not a favorable one. There is no contradiction in the fact that in sepiolids, which always have a well-developed cornea, that closure has been entirely conserved when a secondary, nektonic life-style was adopted (*Heteroteuthis*, Vol. 1, Pl. 19, Figs. 10 and 12, p. 597); this may be related to an ultimate perfection of a cornea already having a watch-glass effect. At any rate, among teuthoids and sepioids the more benthic or littoral forms have a cornea, whereas open primary lids are the rule in nektonic forms. The loliginids, which are continuous swimmers, are more closely related to the coast and to the bottom than the oegopsids (Volume 1, page 168); this is expressed also by their habit of fixating egg masses to a substratum. (The conservation of accessory nidamental glands is probably related to this condition).

333 Another ecological aspect also should be noted: among the octopods (polypodoids) studied in detail, the argonautids and the benthic octopodids are similarly opposed to each other; some of the octopodids again have very large eggs, a very complete embryonic development and a closed primary lid at hatching. In the argonautids with their small eggs and immature "larvae", in contrast, the primary lid remains half open even in the adult, in other words the closure of the diaphragm (Vol. 1, pp. 659, 660 and 726) is not definitive after metamorphosis; in octopodids producing small eggs it is completed subsequently (Textfigs. 116, 121) when the larvae adopt a benthic life-style.

It is not at all certain that the *inhibition of cornea formation* is induced by the *surrounding medium itself*. The latter could be merely the vector of a factor responsible for this effect, or could destroy or *wash away* a factor *inducing* lid closure. The latter is indeed my present assumption: I presume that the intrachorionic fluid normally contains a stimulating agent (secreted by the embryo) that triggers the closure of the lid. (To verify these assumptions I have undertaken experiments about the effects of *hormones* in amphibians, especially *Salamandra maculosa*, since I was located far from the sea at that time; these experiments demonstrated that the surrounding medium can

carry hormones with precise effects, and that the hormone concentration acts on the triggering effect and on the specificity of developmental steps).

Ultimately the determining factor for normal development of the primary lid (like almost the entire complex of developmental stimuli) is provided by *the developing organism itself* (cf. Naef, 1917, p. 29, and citation therefrom p. 37). A peculiarity is that the acting substance is released into the intrachorionic fluid; it indeed seems more familiar to consider hormones as stimulating agents circulating in body fluids.

Most of the controllable *developmental stimuli* probably are produced by neither of the above processes, but by direct *contact* between developed parts and a substratum of still undeveloped parts; in more general terms: by the immediate effect of the condition just achieved on its carrier ("self-differentiation"). For the study of these relationships, the embryos of *Sepia officinalis* provide material essentially as convenient and interesting as amphibian embryos. It is indeed possible to *sever* parts of the embryo even inside the chorion, either by ligation, pinching off or a sort of chiselling using moderately sharp instruments, and to follow the further development of an embryo under such altered conditions. One can thus produce *embryonic regenerates* of arms and tentacular clubs, *doubling* or *fusion* of parts. By ligation of a germinal disc of *Sepia officinalis* at stage II-III, I have thus obtained an embryo that was rather normal dorsally, but ventrally had, side by side, two funnels, two pairs of gills and supernumerary arms (stage XI-XII). Well designed experiments and a careful interpretation of the results will probably yield interesting insights, about which we can say nothing now. Perhaps it will be possible to localize the rudiments, e.g. of the arms, at earlier stages than is possible now from sole observation (p. 248).

In other tentative experiments, I tried to analyze simple *mechanical* relations: it is known that the relative *yolkiness* of the eggs and embryos has been considered to be responsible for many "cenogeneses", i.e. for markedly atypical (altered) developmental processes (p. 38). If the general idea is correct, as I suppose, we have to consider the yolk as a dead nutritive mass, the mechanical effect of which essentially *opposes itself* to the *living developmental effectors* and their tendencies, thus influencing the outer aspect in such a way that the underlying rules of development are obscured. If this effect could be eliminated, either partly or entirely, the resulting aspect would indeed provide an approach to the primary type.

It is in fact possible (see above) to *eliminate a considerable part of the yolk* without altering too much the developmental conditions. One thus obtains stages very sim-

ilar to normal ones in terms of tissue differentiation and organ development, but different in terms of their overall aspect due to the absence of *special peculiarities normally caused by the yolk mass*. The spatial correlation of parts (bauplan) then approaches (prematurely) the anatomical conditions that are normally attained only after resorption of the yolk; thus it *potentially* already is effective at earlier stages (I have made histological sections of these embryos and compared them in detail with normal ones).

The best stages to observe such an effect are stages VII-X (Pl. 15, Figs. 1-4, cf. p. 164); if by simple puncture of the yolk sac at the vegetal pole yolk is allowed to leak out at stage VII, one observes a distinct elevation of the arm rudiments and of the mantle rim; the embryo thus appears to approach stage VIII. Corresponding relations can be seen between stages VIII and IX, and between stages IX and X.

It is also very easy to alter the *second phase of yolk uptake* by the embryos of *Sepia* and *Loligo* (stages XVI-XIX). When the embryo has basically finished its internal differentiation at stage XV, the body itself (Cf. Textfig. 63) contains only a very
335 small amount of dead nutritive material; the typical dibranchiate bauplan can then be visualized in its most simple, synoptical form by going through serial sections. But soon a rapid uptake of yolk occurs, accompanied by rhythmical contractions especially of the umbilical zone (Cf. Pl. 18, Fig. 4), while the body of the embryo remains inactive. Its *viscera* are strongly *compressed* by the rapidly increasing mass of the inner yolk organ, and the typical relations of organs are markedly disturbed. For a beginner, serial sections then become very difficult to "read". It is only following the progressive resorption of this nutritive mass that the primary bauplan of the embryo (stage XX) again becomes clear; it will be fully restored during postembryonic stages, as far as is possible given the advanced developmental stages of individual organs, which have been modified meanwhile.

If the *yolk sac* is entirely *ligated off* (using woman's hair slung around the chorion) at stage XV in *Sepia* or *Loligo* (Pl. 6, Fig. 6; Pl. 16, Fig. 7), the resulting embryos at stages XVI-XVIII appear somewhat feeble, but show an *accelerated* histological and anatomical differentiation of the inner organs, which do not have to cope with the *transient disturbance of the bauplan* that normally occurs during later development. It would probably be possible to raise such embryos to the hatching stage in *Sepia* and in *Sepiola*.

The *first phase of yolk enclosure* (Pls. 3 and 32-33; Textfig. 69) and the subsequent concentration of the embryonic body (leading to the constriction of the yolk sac)

also permit experimental interventions: if one weakens the embryo of *Loligo* at the stage of its maximal extension (by keeping it in too warm, or poorly oxygenated or carbon dioxide rich water), the normal contraction does not take place, but such embryos can be kept alive for several days. Overall aspects thus obtained (Cf. p. 176) are very reminiscent of *oegopside* (Pl. 10, Figs. 1-3): the *yolk sac* remains rudimentary, the arms lie close to the anterior end of the whole, then the eye stalks follow; the funnel complex does not, or only belatedly, reach the mantle sac opening (Pl. 9, Figs. 7-9), and the mantle remains frail and is strongly extended by the still-unused inner yolk. Generally such embryos cannot be raised to the hatching stage.

All these experiments seem to confirm the idea that normal development expresses only part of the dormant potential of an organism, the remaining ones being a sort of reserve which is exploited in the case of emergencies, in an attempt to survive. In the course of phylogenetic adaptation, this reserve also may have offered possibilities for new formations to be assembled largely from a heritage of very ancient forces.

3. Results of General Systematic and Methodological Significance

I.

The special objective of this monograph was a descriptive presentation and systematic (comparative) consideration of a group of ontogeneses in their hypothetical context, i.e. according to their respective similarities. Such an attempt, if it wants to be successful, leads to the formulation of a genealogical tree-like *system*, which can finally be *interpreted phylogenetically* in the sense of the general theory of heredity. It thus expresses the only scientific idea about the phylogeny of the group (p. 14).

Rather than dwelling on the special relations of individual species or genera, one may of course look backwards as it were, and try to formulate the nature of the recognized relations of similarity in general, or at least within a given class (such as the one studied here). One can expect that there are different ways to characterize, compare and summarize them than solely based on the observation that they appear to be linked by definition to well-defined parts (subgroups) of the given diversity of forms. Instead of special systematics we should then get a general theory of system relations, and instead of special phylogenetics, a general theory of phylogeny.

This problem is not new, although its significance has never been fully recognized in published work. It is in fact the logical starting point of any scientific consideration of phylogeny, i.e. of the general theory of heredity and evolution (p. 14). It starts out from the *genealogical tree-like characteristics of the natural system* and aims to answer the question of its cause and origin (Vol. 1, p. 6). If it turns out that the (at first

sight) purely systematic relations could, or do have further general characteristics, then additions to the theory must be envisaged, according to the level, i.e. the degree of generality of the objective evidence on which they are based.

Our starting point for this attempt is defined by the general (spatial-temporal-dynamical) features of developing animals and their relation to systematics and (hence) to phylogeny. The *stock* (of parts) and the *texture* (correlation) of the individual *ontogeneses* have to be analysed to recognize the *characters* by which they differ or coincide in the various groups of the natural system. The quality and quantity of observed formations, their succession and relationship have to be considered again
 377 with respect to their *systemic condition*, and formulations have to be sought that cover all or most of them; the cases studied then appear as examples reflecting general rules, which must be based on certain laws.

The *strongest result of this kind* is the "*law of conservative preliminary stages*" (p. 33). The present part of the cephalopod monograph has been worked out essentially for its exposition (cf. title page of the plates for Volume 2, already published with the first issue in 1921); it has been treated here first, since all the descriptions in this volume were given as further support. This law is supposed to replace the so-called "*biogenetic fundamental law*" in historical morphology and biology. Several books have been devoted to the discussion of the latter, but this discussion has generally remained at the level of vague considerations. To get beyond this stage and cope with the unresolved questions, it seemed necessary to base the discussion on a detailed yet comprehensive treatment of comparative developmental aspects in the framework of a monograph, with the *obligation* to present the results as completely and as perceptually as possible. One may raise the question whether the cephalopods are the most appropriate material to be studied to this end. (Surely a synoptic treatment of a section of vertebrate embryology, especially a clear exposition of the ontogenetics of outer body forms in this most popular and (for us humans) most interesting phylum would have been more effective and more gratifying.) However, in the course of this work the object was determined, and whatever choice might have been made, it would not have influenced the general result if we are talking about laws.

Essentially *related stipulations* certainly are numerous; they cannot be treated comprehensively within the limits of this book. Only a few examples, which virtually imposed themselves in the special part, can be given here. Let us start with a few *positive* statements:

The law of conservative preliminary stages is concerned with the special case of a relationship that can be given a more general significance (pp. 36 and 40), namely, the causal relation of phenomena in the course of development: a conditioning state or factor undergoing modification inevitably drags along the conditioned state, whereas the latter can be modified even in an essentially unaltered situation of conditioning as soon as *one* new factor (stimulus) acts on this starting situation. *So far as* it is possible to demonstrate that certain *preceding* parts and properties clearly *condition subsequent* ones, they must be considered *primary* in systematic-morphological and phylogenetic terms, *apart* from any bodily (*structural* or gestalt-like) *continuity*. Such demonstrations are rarely available and thus do not yet permit a general formulation that would have an impact on the system and phylogeny.

338 The fact that the phylogeny (or systematic position) of very highly evolved forms has always drawn special attention led to the biased opinion that phylogenesis *always* aims at a climax (complication) of organization. This can absolutely not be derived from the totality of systematic relations, even though the predominant groups, which demonstrate the possibilities of a particularly diversified type, may generally owe their situation to such a climax, which therefore characterises its origin. Any *single* structural enrichment of course permits *multiple* losses in the (increased) progeny, be it by direct reversion or by compensatory reductions.

It should be remembered that I have pointed out (ever since 1911, see especially 1913, pp. 358, 362) the *predominance of descending development* and its *morphological characteristics*. Anton Dohrn was probably the first researcher to be struck, especially during his studies of crustacean development, by the peculiar fact that major groups are characterized by a surprisingly profound reduction of organization ("degeneration"); this experience was crucial for his subsequent studies, although it was in some points misleading (cf. Dohrn, 1875, p. iv). When scrutinizing the cephalopod system with this experience in mind, we observe, for example, that among the dibranchiates, the *octopods* are characterized by an almost complete *loss of the shell, of one (prehensile) arm pair, of all buccal arms, of the funnel attachments, of the nuchal gliding apparatus, of the funnel valve, and generally also of the fins*. Among the decapods, the *teuthoids* are characterized by a strong reduction of the phragmone, and among the *sepioids*, the *sepioids* are characterized by its complete loss. In those oegopsid groups in which normally hooks are formed from suckers, this transforming process can be again suppressed in different brachial areas and to different degrees.

In no case are we looking here at declining groups, such as those having found cheap refuge in limicolous life-style, filter feeding or parasitism; or the contrary, we are dealing with ascending groups undergoing progressive specialization, in which the competition between *active* and *aggressive* adaptations and *passive* or *protective* ones has favored the former, especially in the relation between the *muscular mantle* and the *chambered shell*. Whereas in dibranchiates the typically structured muscular mantle merely increases in size and power, without necessarily gaining markedly in terms of morphological differentiation, the loss of the chambered shell (in different variants) represents the suppression of a highly structured apparatus, the acquisition of which must have been much more expensive in evolutionary terms than its reduction.

339 Although the *process* of *degeneration* is not directly observable, not even documented by clear reminiscences in ontogenesis, it is nevertheless easily understandable: it follows the pattern of *neotenic modifications* (Cf. Naef, 1913, pp. 353, 356; 1917; pp. 30, 31, 36, 37); it consists of the repeated omission of ultimate and penultimate stages of development (or growth pulses) in the typical morphogenesis of a part in a given species; such omissions may occur for the benefit of other parts. This process may come in different variants:

a. *Simple neoteny* in which certain modifications of certain parts are omitted (without marked disturbance of other parts). If the larval overall aspect is conserved, as in urodelan neoteny, and the subsequent phases of development are almost completely suppressed, we can consider it as an extreme case ("*habit neoteny*") which is due to the dependence of most of the outer parts on a simple factor (thyroid hormone). *Partial neoteny* (with conservation of some juvenile characters) is much more frequently encountered in morphological series.

b. *Retarding neoteny* in which a heterochronic shift, towards the end of life, occurs in the development of certain parts, the last steps being omitted. It permits any gradation, down to the conservation of only the early rudiment, and ultimately to its suppression. Its counterpart is the earlier appearance of rudiments and the condensation of early development in the course of ascending series (see below).

c. *Paedogenesis*, combined with premature death.

One finds in general that *complicated parts* are *accelerated* in terms of differentiation and growth compared to simple ones. This can be seen particularly in the higher *sense organs* and in the central nervous system, such as the eyes and brain of cephalopods. At a stage like that shown in Textfigure 40 these organs take up an

extremely large part of the embryonic material. Compare also Textfigures 100 and 84—A less generalized observation is that *homonomous formations*, the relative size of which will later be very different (in relation to functional differentiation), are formed from rudiments of *very unequal size at early stages*, rather than from similar sized ones. See the tentacular rudiments of *Loligo* and *Sepiolo* in Plates 2 and 23, respectively. Clearly, this reflects a secondary adaptation of the rudimentary form to the functional state, in the sense of direct development.

But there are some *negative* insights that also are significant: it does *not* appear that, due to a lengthening of development, any ancient *terminal stages* have become
 340 *transitional stages*. Therefore *palingenesis** does not exist in its original sense (pp. 39, 41). Likewise one *cannot* say that characters appearing *early* in development are *unconditionally more conservative* than later ones!

Therefore the "law" of K.E. v. Baer is *not* valid in the sense that characters always appear in the sequence of their respective phylogenetic age (p. 32), i.e. empirically according to their degree of generality (p. 20); yet this idea comes much closer to the true situation than all of the older ones and most of the subsequent ones (influenced by Haeckel). Relatively *special features can be expressed very early*, as demonstrated by certain peculiarities in the embryonic organs of primates, or by the atypical cleavage mode of cephalopods (p. 92). And relatively *general features can be expressed rather late*, e.g. the modification of the hectocotylus within the octopodids: the species characters are long established when the general family character first appears in this part. —Likewise the time sequence of teeth in the individual development of mammals, or the time sequence of arms and suckers in cephalopod development has clearly nothing to do with their phylogenetic sequence.

Ontogenesis provides *no complete "summary"* of phylogeny either. Very *important parts* of older organization, including their rudiments, have completely *disappeared*: the sepiolids do not form anything in the posterior part of the shell sac that could be interpreted as a phragmocone relic; the dibranchiates provide no hint of an earlier existence of anterior gills; the octopods do not provide any direct indication of a fifth arm pair. This is of the greatest methodical significance (See below). There is also *no sign* that parts undergoing reduction would conserve *earlier potentials* in a *latent* state that would still be *more complete* than what is presently expressed. These

* The most recent attempt (A.N. Sewertzoff, 1927) to rescue this popular idea will be discussed and rejected elsewhere.

potentials often may disappear altogether if they are not directly or indirectly involved in the generation of indispensable normal parts.

It is absolutely possible, however, that *phylogeny* refers to *earlier stages*—in strict contrast to the so-called “law of Dollo”; this occurs in the numerous cases where such ancient stages are conserved (as necessary conditions for subsequent stages) in normal development. For example, it is true that the entire larval aspect of urodeles should not be taken as a recapitulation of an ancestor, but it still contains various features that have been inherited from older vertebrate types, so that *certain parts* of the mature Axolotl can be considered to express a reversion to ancestral states: such features are
 341 the continuous *marginal fin*, the open gill slits which are only partly covered by an incomplete *operculum*, and the *sipping mouth* reminiscent of the lungfish type.

Similarly, transitional and terminal elements of descending morphological series can be interpreted in various ways, as will be shown elsewhere. In the reduction of cephalopod shells, we do not encounter *entire ancestral forms*, but we may find *certain traits of them* (See below, p. 364).

It has been stressed several times (pp. 21 and 40) that the temporal correlation of ontogenetic stages may fluctuate strongly (*heterochronies*), and in summary it can be stated here that each embryo and each larva or terminal form represents a *mosaic of phylogenetic old and young* characters, which is due to a network of old and young causal connections, the *encounter of which* cannot be considered an expression of a *comprehensive law* other than the following one: anything occurring in a normal ontogenesis is (or was recently) *useful* for the survival of the given species under the given conditions of life.

II.

The *methodology* of a science is made of those *concepts, supplementary notions* and *principles* that have proved true in the consideration of precise objects. They are not given *a priori*. The tools employed in this work have been sharpened in the course of being used (Cf. Vol. 1, p. 3) and are part of the *essential results*; whether they are entirely new or basically old tools that have been re-established in their original role is of no importance here. Reality lies half-way in between: the pre-Darwinian,

idealistic morphology worked with very imperfect methods; an elaborate system of concepts and principles would indeed have stood the test of the Haeckelian assault.

A systematic presentation is not a protocol of investigation; therefore the methodological results obtained during the present work have been given as an introduction, thus allowing it to be used in subsequent sections. The most significant term is presented in a newly-formulated statement, namely the "*principle of phylogenetic reminiscences*" (p. 41).

342 Much more fundamental, however, is the insight that the *purely conceptual classification* of naturally given objects, especially the order established by the *system* of species, is the indispensable first step of a comparative consideration of observed facts. It opens an access to all the further connections; it is achieved by the most straightforward and reliable means of accurate thinking, devoid of hypothetical complication and confusion (Cf. *Zool. Jahrb. Abt. Anat.*, 1926, p. 406!).

It is from classification that all the other principles are derived, including the principle of phylogenetic reminiscences.

Of even more general nature are the concepts guiding a methodical description and comparison of forms, especially *bauplan*, *ontogenesis*, *homology*, *similarity of plan*, *formative (developmental) norm*, *typical similarity*, and *metamorphosis* (cf. pp. 3-15). The serial arrangement of forms showing a similarity of plan according to aspects permitting us to visualize progression in a certain direction results in the concept of the "*morphological series*". The latter may suggest a phylogenetic process (series of ancestors); but it is obvious that it cannot disclose directly the real process, it can only suggest possibilities.

Morphological series of a special kind are obtained by the combination of the concept of *systematic gradation* with the concept of *type*: if we determine the morphological norm, step by step, for increasingly restricted systematic circles (as in Textfig. 3), a series of representations results that visualize the concept of *morphological gradation*. This concept allows us to obtain an overall picture of a given species or a special part of it at the end of a series of necessary pictures that have been constructed methodically, i.e. based on observation and reflexion, or by visualization and ordering logic. The final pictures appear formally connected to the members of the series; this type of connection is termed a "*morphological reduction*" or a "*derivation*".

Relative to the basic assumptions of the general theory of derivation, this results in a "*representation of phylogeny, namely of morphological grades that must have*

passed through the changing formative norms in the assumed series of ancestors (pp. 14, 30 and 356). Since the naturally existing objects of morphology are ontogeneses, this also is valid for their formative norms and for the complete gradations into which we arrange them; these gradations thus are made of inferred or hypothetically assumed individual ontogeneses.

(Here we disregard the polymorphism of genders or generations which further complicate the picture of a specific type.)

Thus a systematic-morphological consideration *secondarily* becomes a phylogenetic consideration and permits us to relate embryonic and larval formations to a theoretical or hypothetical previous history. The latter is *theoretical* if the systematic relationships are very clear and unambiguous; it is *hypothetical* if the present understanding of these relationships is only tentative.

How far the individual *characters* of an embryonic form can be *traced backwards* (as embryonic characters) in phylogeny depends entirely on a careful comparison, done step by step, among the systematic relatives. We then may be surprised to realize that an embryo, e.g. of *Loligo vulgaris* like that in Textfigure 137, in addition to species-specific features, also combines primary traits of the genus, family, suborder, order, subclass and class, even of the phylum Mollusca—i.e. of grades above which it will rise only subsequently. It is thus inconceivable that an ancestor may have presented them at the adult stage; the wider we draw the systematic circle, the lesser can we consider an extant combination of characters as typical for an embryonic form, nor can we strictly speak about an overall homology of developmental stages in different forms.

The resulting restriction of K.E. v. Baer's law and the further consequences at the level of methodical *principles* were exposed already (pp. 21 and 25); the historical record, which doubtless resides in ontogenesis, is nevertheless profoundly curtailed. This limitation is inevitable if the naturally appropriate *degree of certainty* is to be secured. It must be made clear that ontogenesis is certainly *not complete* as a record, that it tears apart originally synchronous phenomena and *combines heterogeneous ones*; more important, it does not provide information on any stage of a given formation that might have existed *after the ultimate stage* observable in an extant ontogenesis. The embryo of a common loliginid squid does not reveal anything about a belemnite-like phragmocone in an ancestor, and the oegopsid eye does not tell us whether or not the ancestral eye formed a *Loligo*-like cornea. The latter variants are in fact *not*

knowable, and it is therefore it is preferable to admit our ignorance rather than mix some straggling suppositions with methodical insights.

Such mixing unfortunately has occurred with the application of "Dollo's law", which was supposed, especially by paleontologists, to play a role similar to what the "biogenetic fundamental law" aimed at, namely, to provide a base for conclusions that are derived from uncertainty, via uncertain intermediaries, to end in the dark; they cannot claim any scientific value. Suffice it to mention the considerations of Abel (1916) and Karny (1925) about cranchiids and rhynchoteuthid larvae (Cf. above pp. 23 and 199, and Vol. 1, pp. 396-410, 420-427). Of course it is highly *unlikely* that phylogeny, after various detours, returned to exactly one precisely determined organ structure, or that a long lost, complex formation was restored in exactly the same structure. It is even more unlikely that the atoms of a bank-note that was reduced to ashes combine again to restore the previous form. But this is not the subject of a particular law. It is not unlikely, however, that larval or embryonic patterns have the possibility to generate anew the individual characters of which they conserve the more or less faithfully encoded rudimentary form (rather than subsequently modified formations). It can be demonstrated by *systematic comparison* that the inference of such processes is in certain cases virtually inevitable. But such information cannot be provided by an amateurish "method" by which incidentally conserved forms (fossils) are arranged, using some imagination, in family trees that are then used to derive phylogenetic laws.

Atavisms in the above sense are doubtless occurring; they should not be done away with simply as "inhibitory formations". Modern genetics also demonstrate: 1) that ancient *gene combinations* can be restored anew (after a long interruption) as long as the individual genes involved are conserved somewhere in the specific genotype, 2) that an ancient character which became *inhibited* in the course of phylogeny may reappear once the inhibiting factor disappears, 3) that the gene effects undergo fluctuations due to summing up, enhancement, or abatement, so that a lawful restriction of one or even several increases and decreases in parts of animal organization cannot be postulated.

Much like the general theory of derivation starts from the fact of *variability*, a rejection of "Dollo's law" (as a base for the methodical assessment of phylogenetic relationships) must rest on the occurrence of true *atavisms as special cases*. These are represented by 1) abnormal *appearance of rudiments* in individuals of a species if

these rudiments are absent lack in the type of the genus but exist in the type of a (systematically more remote) preliminary stage (which can be considered older on theoretical grounds or by direct demonstration), 2) abnormally *continued development* of rudiments, in contrast to what happens in the type of the genus or family, but in general accord with a (more remote) preliminary stage.

This is practical determination of concepts with an empirical and critical base, following the general principles of systematic interpretation. A directly phylogenetic definition is scientifically contestable. That a character represents *a return of a remote ancestral feature* can be assumed only theoretically, i.e. indirectly, by means of systematic comparison (Cf. p. 363). However, *systematic comparison of real phenomena according to logical methods is thoroughly different from phylogenetic speculation!*

4. Techniques

The present work did not require any particular techniques of uses of investigation; but see Volume 1, pages 805-807; the indications given there also are valid for advanced embryonic stages. For the study of cleavage and mesoderm concentrations prior to the superficial appearance of rudiments, especially chrome acid mixtures were used; they provide very clear pictures from the outset of their action (See also explanation to Pl. 1!). Once the egg (showing a coagulated germinal zone in chrome-acetic acid) is transferred to water, it can be cut across using scissors, and the germinal disc can then be taken off with a pipette and a fine brush, spread on a microscope slide, and finally—after transfer to absolute ethanol or any other appropriate reagent—post-fixed and stained. But this method does not permit preparation of useful whole-mounts beyond stage II-III. Therefore the Plates were drawn entirely after total preparations made with chrome-acetic acid, with cross-checking observations following other preparation techniques. Fixation using the above reagent should not last too long (2-12 hours depending on the species) since the yolk swells and this may lead to rupture of the egg surface; the latter can be avoided or at least retarded by puncturing the egg at the yolk side. The preparations should be rinsed briefly in water and hardened in ethanol. Bouin's solution also permits fine total preparations.

Live eggs are kept in running sea water provided by the general supply of the laboratory, or in still, very clean sea water taken off-shore, kept at relatively low temperatures. The latter condition is essential for embryos taken from their envelopes, which do not develop normally in running sea water from the pipe system of the aquarium*. For actual experiments on single embryos, filtered or artificial sea water will be necessary.

*Scientific Editor: These indications refer to the working conditions at the Naples station in the early part of this century.

5. Literature Index

a) Special literature on cephalopod embryology

The following list contains only literature specially related to embryonic development of cephalopods, some of which were already given in Volume 1. Addenda to the latter will be given in my review on cephalopods for Bronn's Klassen und Ordnungen des Tierreichs (*Bronn's Classes and Orders of the Animal Kingdom*).*

- Appellöf, A., 1887. — On shell formation in *Sepia officinalis* L. Ofvers. Vet. Akad. Förh. **<in Danish>**
- Appellöf, A., 1893. — 3. Remarks on the cephalopods collected during the Norwegian expedition to the northern seas (1876-78) **<in German>**
- Appellöf, A., 1894. — The shells of *Sepia*, *Spirula* and *Nautilus*. Studies on their structure and growth, Kgl. Svenska Vet. Akad. Handl. vol. 25. **<in German>**
- Appellöf, A., 1899. — On the occurrence of inner shells in eight-armed cephalopods (octopods). Bergens Mus. Aarsber. f. 1898. **<in German>**
- Bather, F. A., 1888. — Prof. Blake and Shell-growth in Cephalopoda. Ann. Mag. N.H. (6), vol. 1
- Bather, F.A., 1894. — Cephalopod beginnings. Nat. Sc., vol. 4.
- Bather, F.A., 1895. — The habits of the young *Sepia*. Journ. Malac., vol. 5
- Bergmann, W., 1902. — Investigations on oogenesis in annelids and cephalopods. Zeitschr. wiss. Zool., vol.73. **<in German>**
- Bergmann, W., 1903. — On the structure of the ovary in cephalopods, with some complements on its differentiation. Arch. f. Naturg., vol. 67. **<in German>**
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- Bobretzky, N.W., 1877. — Investigations on the development of cephalopods. Nachr. Ges. Freunde Nat. Moskau, vol. 24. **<in Russian>**
- Brooks, W.K., 1880. — The development of the squid (*Loligo pealei* Les.). Anniv. Mem. Boston. Soc. N. Hist.

*Scientific Editor: All the titles of articles and books are cited here in English. References were not verified for the translation, and no pagination is given (as in Naef's reference list).

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- Chun, C., 1903. — *Rhynchoteuthis*, a peculiar juvenile form of cephalopod. *Z. Anz.*, vol. 26 **<in German>**
- Chun, C., 1904. — Juvenile octopods in which the whole body surface is covered with tufts of setae; *Pterygioteuthis* with hectocotylization of the left ventral arm. *Verh. D.Z. Ges.*, 14. Annual meeting. **<in German>**
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- Férussac, A.E. 1835-48. — A general and particular natural history of living and fossil sucker-bearing cephalopods. Paris (most of this work, largely written by d'Orbigny, was published in 1839). **<in French>**
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b) Literature on general morphology and phylogeny of molluscs, and on the relation of the cephalopod type to the other classes of the phylum

It should be mentioned here that several earlier papers by the author were published during the preparation of this work; the article of 1924 ("Studien zur generellen Morphologie der Mollusken. 3. Teil: Die typischen Beziehungen der Weichtierklassen..."), which appeared in *Ergebnisse und Fortschritte der Zoologie*, vol. 6) provides a fairly complete list of important recent and older publications. A complete reproduction of this list would be redundant. The following list contains only the most important articles or work that was published in the most recent years.

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c) Literature on the fundamental concepts of systematic morphology and the law of conservative preliminary stages

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IV. ATLAS

37 Plates

On the Embryology of Cephalopods of the Bay of Naples

OVERVIEW:

Plates 1-7:	<i>Loligo vulgaris</i>
Plate 8:	Oegopsid X
Plates 9-12:	Ommatostrephid Y
Plates 13-22:	<i>Sepia officinalis</i>
Plate 23:	<i>Sepiola</i> and <i>Sepietta</i>
Plates 24-30:	<i>Octopus vulgaris</i>
Plate 31:	<i>Tremoctopus violaceus</i>
Plates 32-36:	<i>Argonauta argo</i>
Plate 37:	<i>Argonauta</i> and <i>Ocythoë</i>

These plates present an attempt to visualize a series of ontogeneses, with homology of stages as precise as possible, in order to illustrate the basic view that systematic morphology deals with the comparison of ontogeneses. Along with the numerous textfigures, they provide carefully selected material for a critical assessment of the so-called "biogenetic fundamental law".

Note: These plates were already published with the first issue of the monograph (1921), together with the plates belonging to the first volume (Systematics).

General List of Abbreviations

ad	mantle adductor	km	gill (Plate 27, Figure 2 should read <i>kn</i> !)	st	statocyst
ak	eye chamber (orbita)	kn	funnel attachment	su	protective membrane
al	outer lip	kp	head	ta	tentacle pouch
an	anus (in Plate 2, Figure 4, the upper left should read <i>au</i> !)	kr	gill retractor	tb	ink sac
ap	Arteria pallialis posterior, or else: orbital pore	ks	secondary edge of germinal disc (Plate 18, Figure 3 should read <i>kb</i> !)	td	funnel gland
ar	arm crown			te	funnel corner
as	Arteria siphonalis	kv	branchial vein	tk	tentacular club
at	arm funnel connection	lb	liver	tm	medial piece of funnel tube
au	eye (different parts)	li	eye lens	tn	tentacle
ax	body axis (middle piece)	ma	mantle	tö	funnel opening
ba	cheek-hump	mb	medial band of germinal disc	tr	funnel tube
bt	buccal funnel pillar	mf	medial field of germinal disc	ts	funnel septum
ca	=ea	mh	mantle cavity	tt	funnel pouch
ch	chromatophore	mk	buccal cone	uk	lower beak
cl	central gap of germinal disc	mr	Musculus rect. abdominis	va	venous appendages
co	cone of gladius, or corresponding gap in muscular mantle	ms	mantle septum	vb	anterior connecting piece of primary lid
da	yolk artery	mu	mouth, primary buccal edge	vc	Vena cava
dc	=de	na	umbilicus	vd	forearm (Plate 14, Figure 2 should read <i>vr</i> !)
de	dorsal mantle corner	nd	nidamental gland	ve	ventral mantle corner
dh	yolk envelope	ni	kidney	vk	in Plate 30, Figure 7 auricle, elsewhere ventral ocular edge
dk	dorsal ocular edge	nk	nuchal attachment (in Plate 2, Figure 4, the arrow line is partly indistinct!)	vl	Vena pallialis posterior
dl	glandular line	np	kidney pore, kidney papilla	vm	ventral mantle slit
dm	dorsal mantle slit	nt	seam	vp	Vena pallialis lateralis
do	yolk sac, yolk mass	pd	pericardial gland	vr	annular thickening of germinal disc (meso-endoderm)
dv	yolk vein	pf	1-5 arm pillars (counted from dorsal to ventral)	vs	vein limb (branch of V.c.)
dz	yolk cells	pk	primary head cover	wk	white body
ea	embryonic body	pl	primary lid	wz	kin warts
ed	hindgut	po	primary pupil	z, y, x, w, v, u etc.	mark certain, individually varying points on the embryo (Cf. Plate 1)
es	terminal tip of mantle sac	pr	proostracum, or corresponding gap in muscular mantle	d	or sometimes b, indicates the posterior end of the dorsal "ocular edge"
fa	vane of gladius	ps	=ms	v	posterior end of ventral "ocular edge" (Cf. Plate 6, Figure 4!)
fe	"window" (fenestration)	pu	pupil	p	position of primary pupil, pore of primary eye vesicle (Plate 2, Figure 5)
fl	fin	ra	marginal rays of germinal disc	n	scar of fusion
fr	frontal field	rh	rachis of gladius	t	funnel corner
gb	waistband	ro	olfactory organ	s	scar of shell pore
gd	poison gland	rs	marginal part of fin	A-D	the four cleavage octants of one side (Plates 1 and 24)
gl	gladius	rz	marginal cell	I-V	the five arms of one side, numbered from dorsal to ventral (Pl. 19, Fig. 5; Pl. 9, Fig. 1 should indicate IV instead of III!)
hb	posterior connecting piece of primary lid (Plates and 32 should read <i>hl</i> !)	rt	funnel retractor	X	medioventral arm rudiment (?) (Pl. 2, Fig. 5).
hl	posterior gap of embryonic body	se	shell epithelium		
hm	=hb	sf	shell fold		
ho	Hoyle's organ; 1 medial, 2 lateral branch	sg	Ganglion stellatum		
hz	heart	sh	web		
il	inner lip	sk	secondary lid		
ir	iris	sl	lateral line of mantle		
ka	head anlage (different parts)	sm	buccal mass		
kb	branchial band	sn	mantle nerve		
kh	branchial heart	sp	shell pore		
kl	funnel valve	sr	subradular organ		
		ss	swimming membrane, or lateral edge of ventral arm		

The time or stage indications for embryos figured are to be considered as approximations. They do not always refer to a single egg mass, since eggs spawned in the aquarium do not develop normally to hatching when disturbed for the needs of observation; moreover the duration of development depends on temperature (season). (See also page 88.)

Corrigenda: Plate 5 shows erroneous numbering. Exchange 3 and 5, 4 and 6!—Plate 28, Figure 9 shows stage XVII; Plate 30, Figure 7 shows stage XIX-XX.

Naef—Cephalopoden
Plates of the 2nd Volume
(Developmental History)

These plates present an attempt to visualize a series of ontogeneses, in order to illustrate the basic view that *systematic morphology deals with the comparison of ontogeneses*. They provide carefully selected material for a critical assessment of the so-called “biogenetic fundamental law”; this material was used for the preparation of the text of this volume, and it will be further exploited in future theoretical and methodological articles.

Plate 1: Cleavage and formation of germinal layers in *Loligo vulgaris*. 30× natural size.

Eggs viewed from the animal (posterior) pole. The formative plasm appears light, the yolk dark due to chrome-acid treatment, thus providing a better visual contrast.

- Fig. 1. Two cell stage, 6 hours after egg laying, which is first followed by maturation and fertilization processes (Cf. Plate 24). u: yolk; y: first cleavage furrow, tapering out on the yolk surface (v); w: ray of formative plasm (very thin!); x: body of left blastomere; z: nucleus.
- Fig. 2. Four cell stage (7 hours). x=v of Fig. 1; y: central gap.
- Fig. 3. Eight cell stage (8 hours). A-D: the left octants. Same designation throughout!
- Fig. 4. 16 cells (10 hours); x: micromere derived from A; y: micromere derived from D. The octant D appears darker (poorer in cytoplasm)
- Fig. 5. 32 cells (12 hours). x: micromere derived from B; y: ...from C; z: ...from D.
- Fig. 6. 64 cells (14 hours). The furrows (x) tapering out on the yolk surface become broader, the rays of the macromeres (y) become narrower; the micromeres derived from D form a distinct (also during subsequent stages) cell plate (z) called the "medial field" of the germinal disc, giving rise to the shell epithelium. The dibranchiate features seem to be correlated with the small size of the octomeres D that have to be considered in relation to the D tetramer of other molluscs, to which they apparently correspond. (Similar considerations can be made for A!).
- Fig. 7. Ca 170 cell stage (17 hours), comparable to a blastula. y: "medial band", a double row of micromeres derived from D; w: their rays of cytoplasm. Stage I*
- Fig. 8. Ca 700 cell stage (24 hours). Transition to the modified gastrula (See text!). v: macromeres moving outwards on the rays along with subdividing. This process leads to the following stage.
- Fig. 9. Over 1000 cells (27 hours). The germinal disc (by a process lying half-way between delamination and epiboly) has become divided into three elements: 1. the ectoderm, a distinct cell layer with circular outline, 2. the endo-mesoderm, an irregular cell mass, consisting of (about) eight portions on either side, that has been shifted under the rim of the ectoderm (blastopore) (See the text for its morphological interpretation), 3. the yolk cells in radial arrangement.
- Fig. 10. Stage II (32 hours). The ring of endo-mesoderm (x-x) appears closed except for a ventral gap that corresponds to the D octomeres. The latter, which can be recognized from the two parallel rays on the yolk (y), are apparently not involved in the formation of the lower germinal layer.
- Fig. 11. Stage II-III (36 hours). Endo-mesoderm coming in from the sides also now appears in the ventral gap (y below). The rim of the ectoderm (w) moves outwards, covering the bases of the rays (y at the right) which remain visible through the thin marginal part (v) of the germinal disc. The annular mass of endo-mesoderm grows towards the center, so that the dark central gap becomes smaller and smaller.
- Fig. 12. Stage III (40 hours). The above-mentioned process continues. The yolk rays are progressively retracted and will finally disappear (Plate 2) below the germinal disc; the first to go are the small cells derived from the D octomeres (y).

*The stages are numbered in Roman numerals I-XX, starting from the achievement of a unilayered germinal disc and leading to the hatching stage; disregarding the more or less marked heterochronies, these stages can be considered "homologous" for the different ontogeneses.

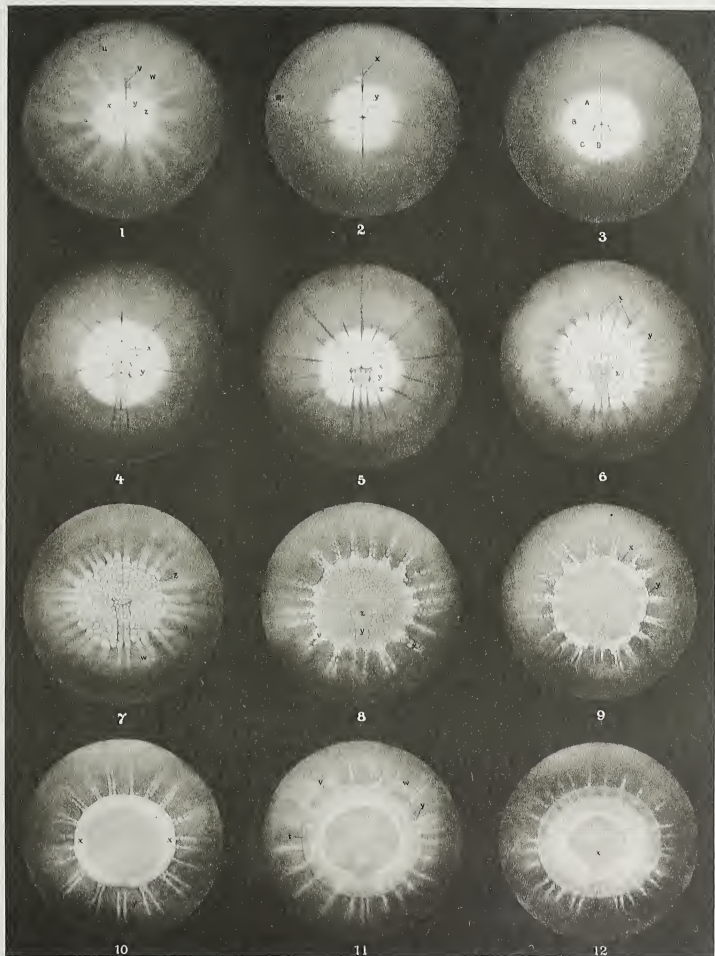
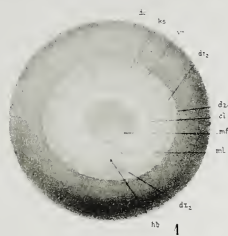


Plate 2: Further differentiation and folding of the germinal disc in *Loligo vulgaris*.
30× natural size.

The light-dark contrast is primarily due to the light coloration of the formative plasm, as in Plate 1; subsequently mesoderm concentrations rise as distinct organ rudiments above the level of the remaining parts.

- Fig. 1. Stage III (45 hours, poor representation!). The ring of endo-mesoderm is broader and ventrally still shows an indentation (hb) as the last trace of the ventral gap (up to Figure 4).
- Fig. 2. Stage IV (3 days old).
- Fig. 3. Stage V (4 days old). Only a narrow zone of the free yolk surface remains visible in apical view, since the germinal disc is now cap-shaped and grows over the yolk. The position of the anus (an) appears as a concentration of endoderm cells. The embryonic body and the yolk envelope (dh) are distinct from each other.
- Fig. 4. Stage VI (5 days old). Cloudy organ rudiments appear and become increasingly distinct.
- Fig. 5. Stage VII (6 days old), these rudiments become prominent.
- Fig. 6. Stage VIII (6 1/2 days old). The organ rudiments form distinct folds.
- Fig. 7. Stage VIII-IX (6 3/4 days old).
- Fig. 8. Stage IX (7 days old).
- Fig. 9. Stage IX-X (7 1/2 days old).
- Fig. 10. Stage X (8 days old).
- Fig. 11. Stage X-XI (8 1/2 days old).
- Fig. 12. Stage XI (9 days old).

Note the relatively late development of the funnel tube rudiment (tr) compared to the funnel pouches (tt) and arms, the relation of the fin rudiments (fl) to shell fold, the appearance of the arm pillar rudiments (pf 1-5).



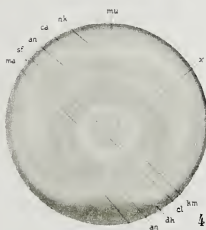
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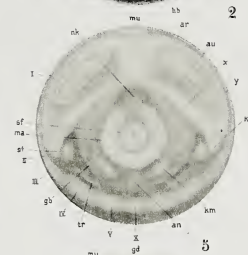
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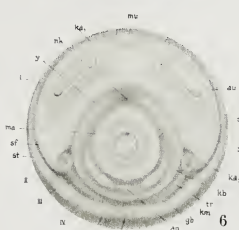
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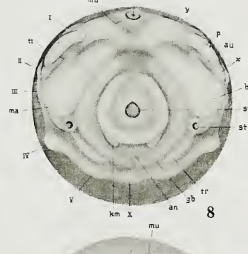
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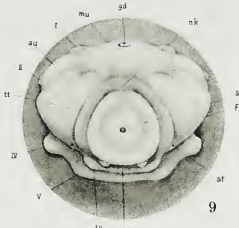
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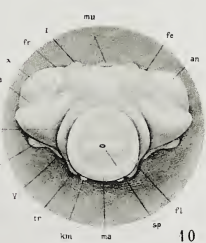
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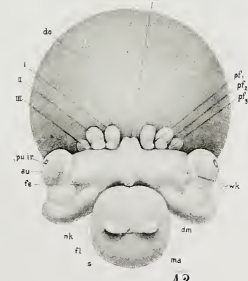
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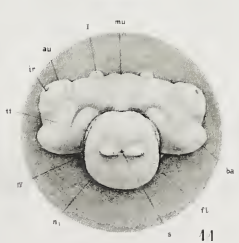
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Plate 3: Folding stages in *Loligo vulgaris*.

30× natural size, in lateral, ventral and dorsal view.

Figs. 1-3. Stage VIII (Cf. Plate 2, Figure 6), 6 1/2 days old.

Figs. 4-6. Stage IX (Cf. Plate 2, Figure 8), 7 days old.

Figs. 7-9. Stage X (Cf. Plate 2, Figure 10), 8 days old.

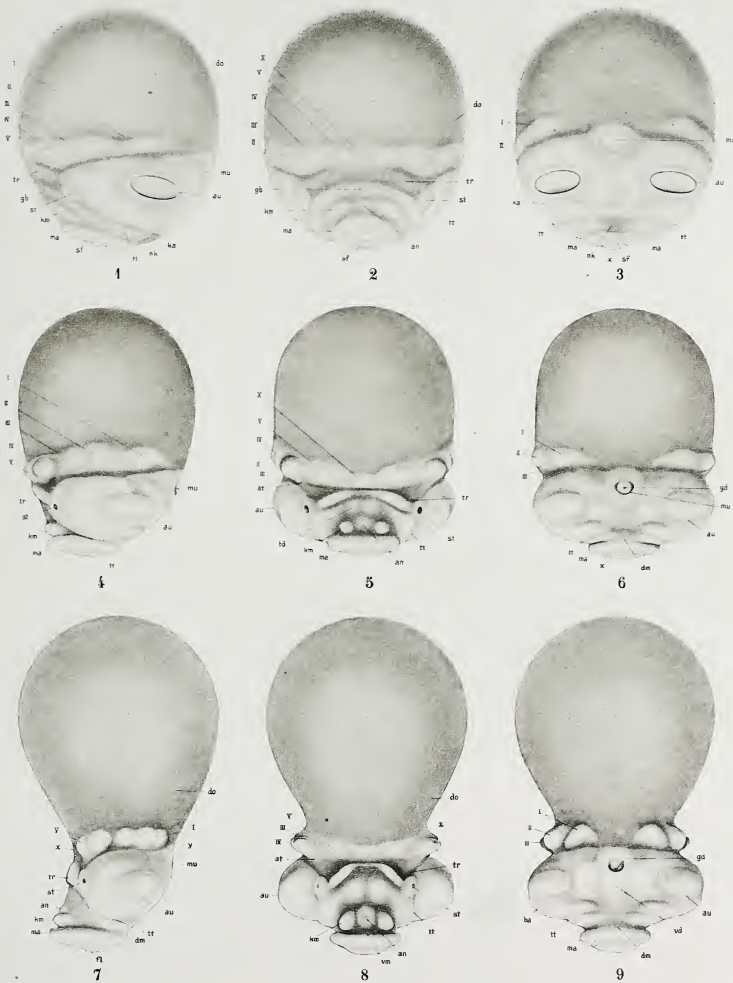


Plate 4: Primary structuring of the cephalopod body in *Loligo vulgaris*.
30× natural size, in lateral, ventral and dorsal view.

Figs. 1-3. Stage XI (Cf. Plate 2, Figure 12), 9 days old.

Figs. 4-6. Stage XI-XII. 9-9½ days old.

Figs. 7-9. Stage XII. 10 days old.

Note the folding over of the mantle organs, the formation of the funnel, the posterior growth of the arm pillars, the invagination of the mouth between the dorsal arms.

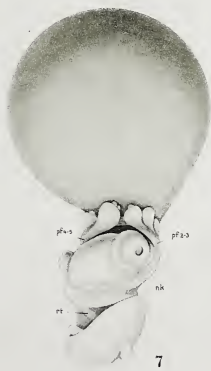
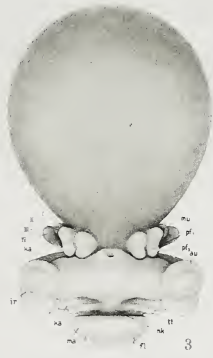
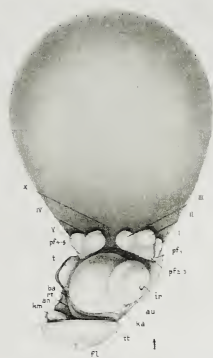


Plate 5: Definitive structuring and modification of the cephalic organs in *Loligo vulgaris*.

30× natural size.

- Figs. 1 and 2. Stage XIII (11 days old). Note the posterior lengthening of the arm pillars, which turn their ventral (vk) and dorsal (dk) ocular edges towards the eye.
- Figs. 5 and 6. (NB: corrected numbering!). Stage XIV (12 days old). Continuation of this process.
- Figs. 3 and 4. (NB: corrected numbering!). Stage XV (13 days old). Continuation of this process.
- Fig. 7. Stage XVI (14 days old). Complete primary lid fold.
- Figs. 8 and 9. Stage XVII (15 days old). Contraction of the primary lid over the eye.
- Fig. 10. Stage XVII-XVIII (15 1/2 days old). The contraction is definitive.

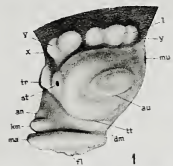
The mouth disappears completely between the dorsal arms (Figures 2 and 4). The gladius shines through the integument in Figure 9, already showing the typical teuthoid shape.

Plate 6: Development of the lateral aspect in *Loligo vulgaris*. 30× natural size.

Note the structure of the primary lid, which is made of four parts: dorsal and ventral ocular edges (Figure 4: dk and vk), the anterior (Figure 2: x) and the posterior "connecting piece" (Figure 7: v-d). These connecting pieces contribute only minor parts of the annular fold. But see the Sepioidea (Plate 16, Figure 5; hb; Plate 23, Figure 5: hb, Figure 2: vb).

- Fig. 1. Stage X (8 days old).
- Fig. 2. Stage XI (9 days old).
- Fig. 3. Stage XII (10 days old).
- Fig. 4. Stage XIII (11 days old).
- Fig. 5. Stage XIV (12 days old).
- Fig. 6. Stage XV (13 days old).
- Fig. 7. Stage XVI (14 days old).
- Fig. 8. Stage XVII (15 days old).
- Fig. 9. Stage XVIII (16 days old).

At stage XVII-XVIII, the primary lid can be opened easily; subsequently it remains closed and leaves only a very narrow pore (Plate 7, Figure 1).



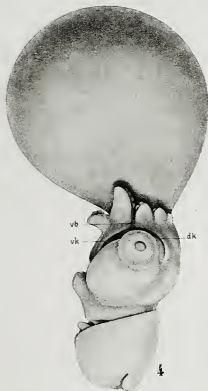
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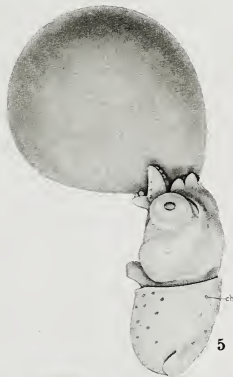
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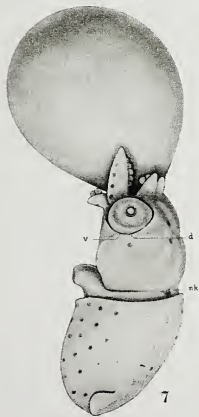
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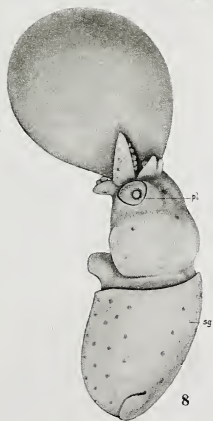
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Plate 7: The mature embryo of *Loligo vulgaris* at hatching, after about 21 days of development.

Figs. 1-3. Three aspects. $24\times$ natural size.*

Fig. 4. Similar specimen after removal of the ventral part of the mantle. For further explanation, see the Textfigure below:

a) Newly-hatched animal, $15\times$ natural size, drawn after the transparent, living animal, figure completed after preserved specimen. b) Arm crown of an advanced embryo, shortly before

hatching, after removal of the outer yolk sac (at d). Above the scar (d) lies the mouth (m). The suckers (s) are not yet numerous, they are still lacking on the dorsal arm; the buccal lappets (1-4) are barely visible as small, flattened papillae; I-IV: arms; T: tentacle. The main figure shows: the small yolk sac remainder (Do) between the arms; the small, stump-like pointed arms (A_3, A_4), between which the tentacles (Tt) project; the web (Sh) between the 3rd and 4th arm, limiting the still shallow tentacle pouch; the eye balls (Au) in the closed orbital cavity (AK, hatched) and its pore (Po) next to the cornea (Co); the olfactory tubercles (Ro) are low, oval elevations on the ventral side of the head; the funnel adductors (Ad); the funnel complex with the barely visible funnel attachments (Th, hatched) and the ventral parts of the funnel gland (Td); the anal papilla (Af); the Vena cava (Vc), hindgut and ink sac (Tb); the funnel retractors (Tr); the gills with alternating gill lamellae, the branchial spleen (Km) forming a solid strand in the gill axis, the branchial bands (Kb) which are still limited to the basal part of the organ; the branchial hearts (Kh) with their appendages (Pd) and the sac-like vein branches (Vs), which receive, from the posterior side, the expanded Venae palliales posteriores (z); the Aorta posterior (x) and its bifurcation into the Arteria pallialis medialis and posterior (y), respectively; the rounded, laterally projecting fins (Fl), across which the lateral branches of Hoyle's organ (Ho) are visible (dotted). Go: gonad rudiment; Di: inner yolk sac; Bl: caecum; Ma: stomach; Cö: coelomic pouch containing the branchial heart; Vk: auricle; Hz: systemic heart; Kv: branchial vein; Ns: kidney sac; Rd: posterior rim of funnel tube; Me: ventral mantle rim corner; Mu: superficial, straight cephalic muscle; Pd: stalk of the eye inside the orbita (AK).

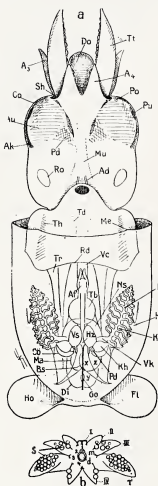
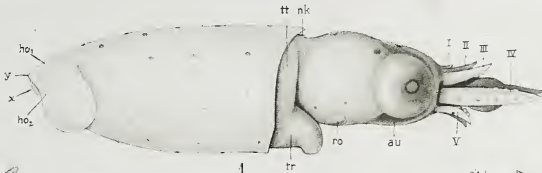


Fig. 5. Head of specimen shown in Figure 1. $36\times$ natural size.

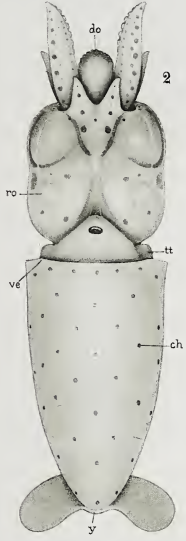
Fig. 6. Mantle sac at stage XVII illustrating the typical shape and insertion of the gladius, which is less distinct in the mature embryo. $50\times$ natural size.

*Scientific Editor: The size indications on the plate correspond to the original plate size (100%), those given here in the translated explanations take account of the size reduction by 1/6 (to 83.5%) of the plates for the English language edition.



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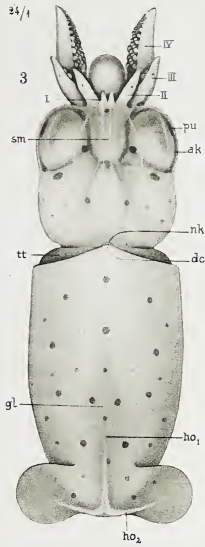
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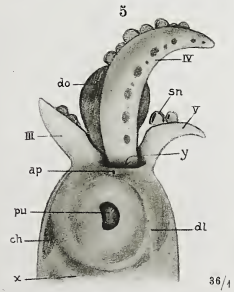
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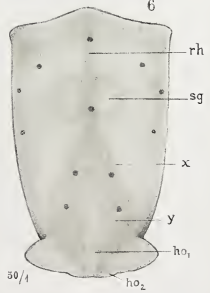
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Plate 8: Embryos from a floating egg mass of oegopsid x. 33× natural size.

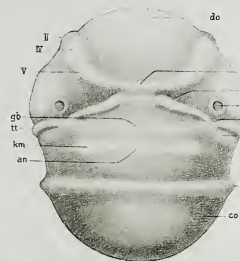
These embryos probably belong to either *Calliteuthis* or *Histioteuthis*, other forms being virtually excluded for reasons of size and others.—The oegopsid features are clear from comparison with Plates 9-11 and with Grenacher's embryo, although the latter shows some peculiar features of its own. Note the reduction of the outer yolk sac.

Figs. 1 and 2. Stage VIII-IX (Cf. Plate 3 and consider the similarity that would appear with the loliginid embryo if the yolk sac of the latter were contracted so as to pull the anlage of the embryo proper across the yolk. Similar products can be generated without mechanical intervention).

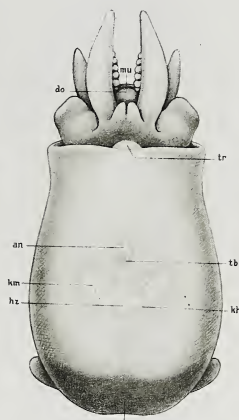
Figs. 3 and 4. Stage X.

Figs. 5 and 6. Stage XVI.

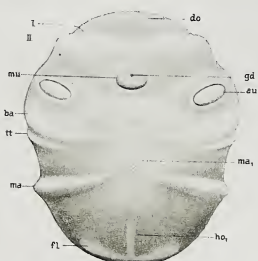
Figs. 7 and 8. About stage XVIII (hatching stage).—Striking heterochronies are visible in the eye, which is reminiscent of the *Loligo* eye at stage XIV (Plate 5, Figure 5), whereas the mantle and funnel are already functional. This is a highly interesting oegopsid larva. The relation between the muscular shell and the mantle is particularly remarkable; it is significant for the understanding of teuthoid shells, indeed of dibranchiate shell insertion in general. The large, scoop-shaped cone (co) surrounds the broad posterior end; it is easy to imagine a transition into an initial chamber of a belemnoid (Volume 1, Textfigure 36). The position of the fins, set far apart on the outside of the cone, also is typical. Anteriorly the cone grades into a narrowing proostracum and thus exhibits a metateuthoid character. It is significant that the tip of the proostracum is flanked by the stellate ganglia (Cf. Vol. 1, p. 146, Textfig. 62).



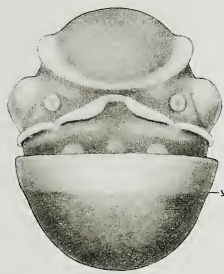
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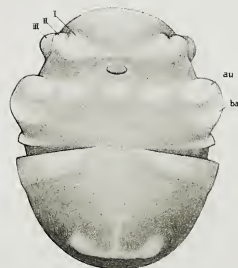
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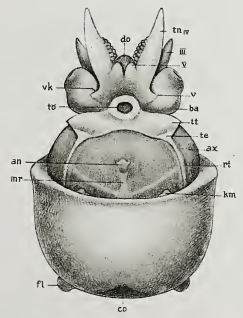
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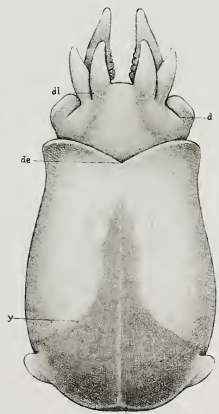
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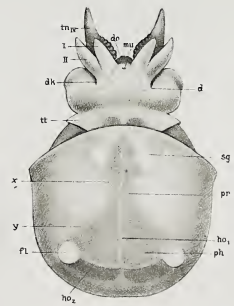
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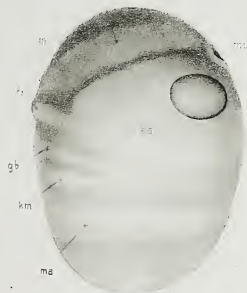
Plate 9: Embryos from a floating egg mass of ommatostrephid y.

(Species identification impossible) 70× natural size. See the general remarks in Plate 8.

Figs. 1-3. Stage VIII.

Figs. 4-6. Stage X.

Figs. 7-9. Stage XII.



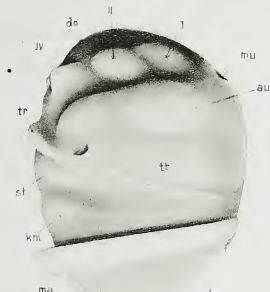
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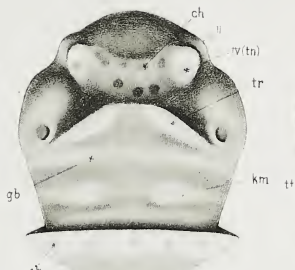
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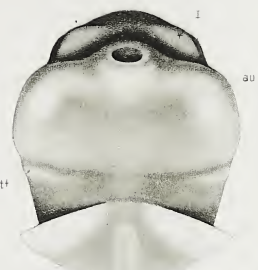
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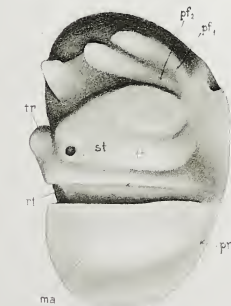
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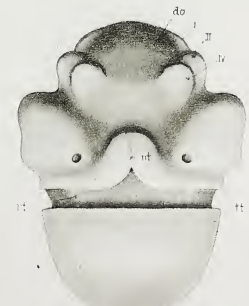
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Plate 10: Embryos of ommatostrephid y. 70× natural size.

- Figs. 1-3. Stage XIV. Note the retardation of the ocular edges (Cf. Plate 6) and the topography of the mantle sac (Pl. 8, Figs. 7 and 8), and the characteristic lack of arm rudiments III (that would be situated at vb) and V (See Fig. 2), which is typical for oegopsids.
- Figs. 4-6. Stage XVI. Here the tentacular shafts begin to fuse together (at nt in Fig. 5).

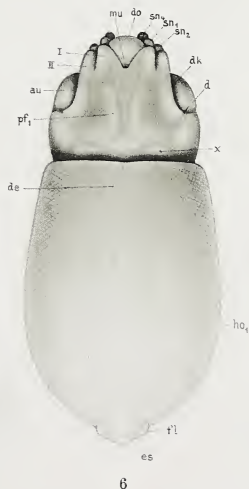
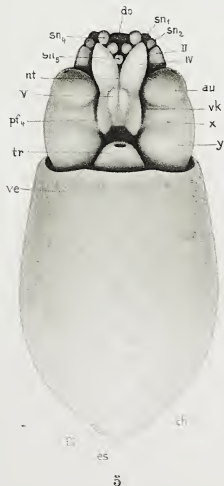
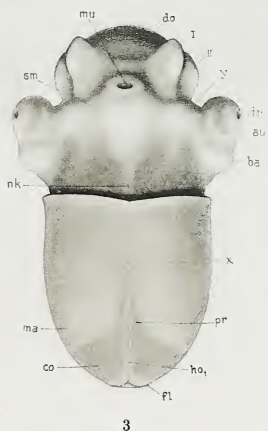
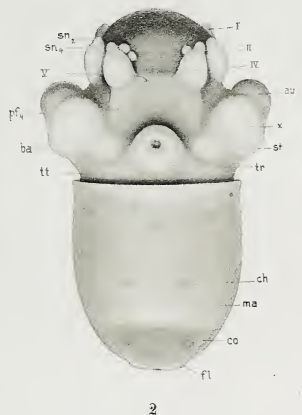
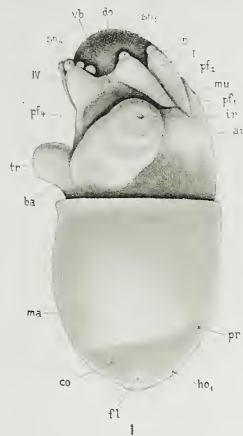


Plate 11: Embryos of ommatostrephid y, 70× natural size.

Figs. 1-3. Stage XVIII. Tentacles fused together, primary lid fold complete (contrast: Plate 8!)

Figs. 4-6. Stage XX. After hatching (Cf. Vol. 1, Pl. 19, Figs. 1 and 2). A typical ommatostrephid "rhynchoteuthion larva"!

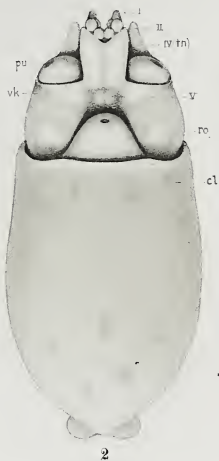
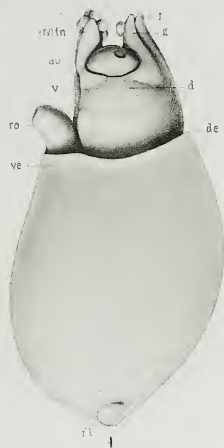
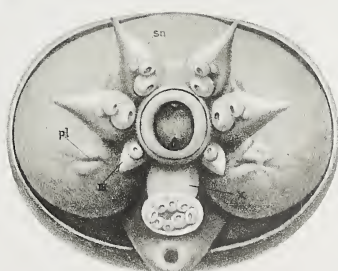
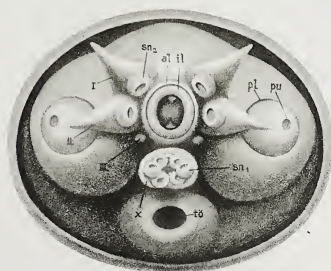
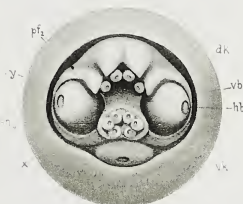
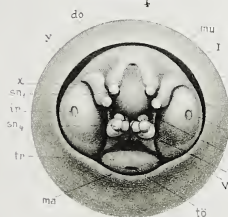
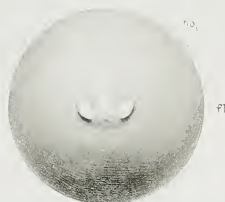
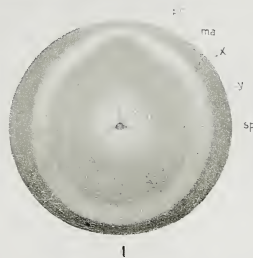


Plate 12: Embryos of ommatostrephid y. 70× natural size.

- Figs. 1-6. The stages VIII, X, XII, XIV, XVI, XVIII seen from the caudal end. Cf. Plate 2 to assess the development of the muscular part (light) and the shell part (dark) of the mantle sac rudiment, the development of the fins (fl) in the area of the shell pore (sp) and subsequent organ of Hoyle (ho). Only little is left of the cone, namely the zone immediately adjacent to the fin rudiments.
- Figs. 7-9. The stages XVI, XVIII and XX seen from the anterior end. Note the incomplete primary lid folds in Figure 7, the relation of the mouth to the yolk sac relic, the four stump-like arms, each with one sucker rudiment (sn), the still separate tentacles (tn) with four suckers each (all of which are typical, early larval ommatostrephid features).
- Figs. 10-11. Post-embryonic development of the buccal area in ommatostrephids. Two rhyngoteuthion stages from the plankton of the Bay of Naples. 42× natural size. The arm crown, which surrounds the mouth (instead of a yolk sac), is completed by the appearance of arm rudiments III, which subsequently grow normally (Cf. Vol. 1, Pls. 5 and 6).

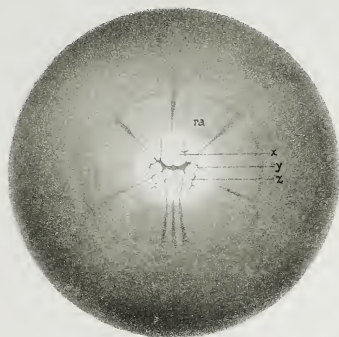


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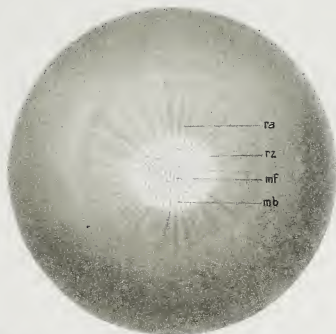
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Plate 13: Cleavage and germinal layer formation in *Sepia officinalis*. 16× natural size.

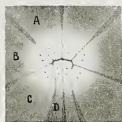
- Fig. 1. 28 cell stage (30 nuclei); x, y, z: micromeres.
Fig. 2. 8 cell stage (16 nuclei) like Plate 1, Figure 3.
Fig. 3. 16 cell stage (30 nuclei); x: first cleavage furrow; y: fourth cleavage furrow, differing from *Loligo* (Pl. 1, Fig. 4).
Fig. 4. 29 cell stage (30 nuclei) (variant y: belated blastomere).
Fig. 5. More than 100 cells. Blastoderm
Fig. 6. More than 800 cells. Stage I-II at transition to endo-mesoderm formation. In the sepioids (including *Sepiolo* and *Rossia*!) the multiplying cells form a complete, narrow ring around which the yolk cells (y) are situated, the central circular plate (x) being the ectoderm.
Fig. 7. Stage II. The ring of endo-mesoderm grows broader.



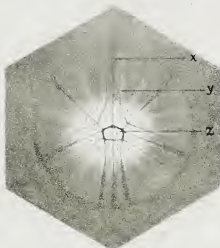
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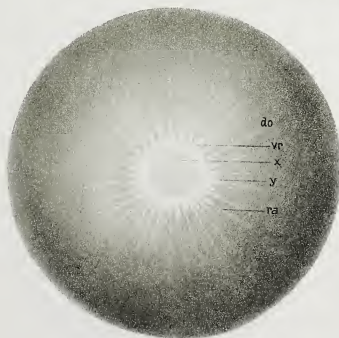
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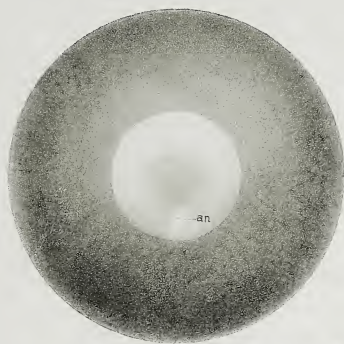
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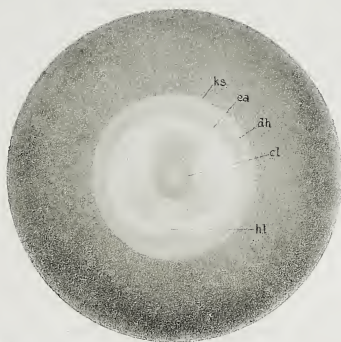
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Plate 14: Differentiation of the germinal disc in *Sepia officinalis*. 16× natural size.

- Figs. 1 and 2. Stages II and II-III. The germinal disc is now retracting the yolk rays (Pl. 1, Figs. 10 and 11).
- Fig. 3. Stage III-II. This is achieved relatively earlier than in *Loligo*. A light dot marks the position of the anus (as in subsequent stages).
- Fig. 4. Stage III (Plate 2, Figure 1). The somewhat more solid structure of the germinal disc explains in part the differences from *Loligo*; these differences disappear in subsequent stages.
- Fig. 5. Stage IV.
- Fig. 6. Stage V.
- Fig. 7. Stage VI.



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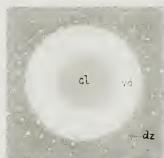
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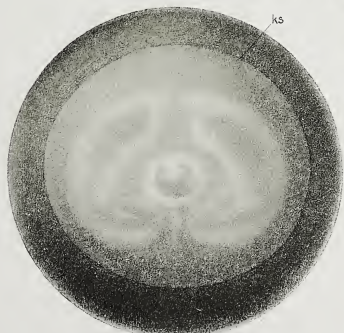
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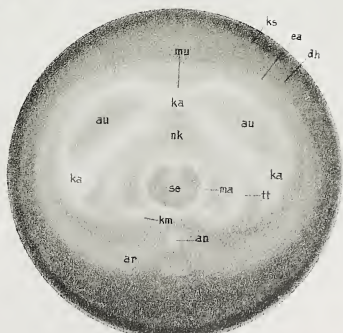
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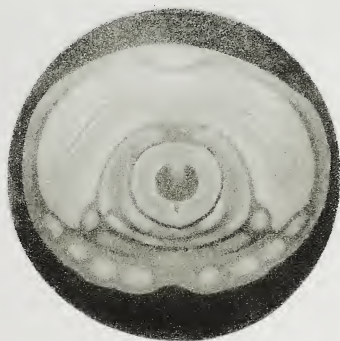
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Plate 15: Folding up of the germinal disc in *Sepia officinalis*. 16× natural size.

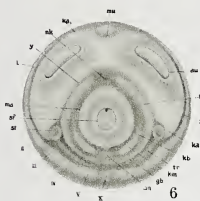
- Fig. 1. Stage VII. Still nearly flat. Due to the preparation (See Plate 1) the mesoderm concentrations become visible.
- Fig. 2. Stage VIII. The rudiments appear as folds and ridges, producing a picture very similar to *Loligo* (Figure 6). The arm rudiments appear bipartite as in all the other sepioids (Cf. Pl. 23).
- Fig. 3. Stage IX. Eye and shell folds contract. On the latter the material for the fins becomes prominent; subsequently this material is arranged around the inverted-T-shaped scar, which marks the prospective organ of Hoyle (Cf. Plates 2 and 12).
- Fig. 4. Stage X. The germinal disc contracts.
- Fig. 5. Stage XI. This contraction pulls the peripheral parts under the central ones.
- Figs. 6 and 7. *Loligo* embryos (VIII and IX) for a comparison (See Pl. 2, Figs. 6 and 8).



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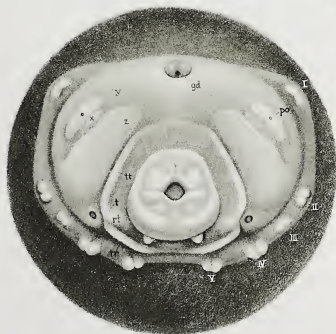
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Plate 16: General structuring of the embryo in *Sepia officinalis*. 16× natural size.

- Fig. 1. Dorsal view of stage XI-XII. $x = hb$. This formation is very conspicuous at early stages (Plate 23).
- Fig. 2. Dorsal view of stage XII (Cf. Plate 4, Figure 9).
- Fig. 3. Dorsal view of stage XII-XIII. $y = fr$, $x = wk$ (Cf. Plate 2, Figure 12).
- Fig. 4. Ventral part of arm crown at stage XII. The sucker rudiments become differentiated from the tip to the base of the arm. x : longitudinal ridge; y : transverse papillae; w : rounded papillae in zigzag arrangement; z : yolk margin (Cf. Plate 21).
- Fig. 5. Dorsal view of stage XIII (Cf. Plate 5, Figure 2).
- Fig. 6. Dorsal view of stage XIV. x : posterior limit of the "head cover" formed by the arm pillars; y : depression between the eye balls and the rudiments of the white body; z : position of the submerged mouth.
- Fig. 7. Dorsal view of stage XV. The dorsal ocular edge has reached the posterior connecting piece at d . x - y : limit of head cover.
- Figs. 8 and 9. Aspects of stage XVI. End of the most important organogenetic processes and the general surface differentiation. The chromatophores, the muscular activity, the heart beat, etc. give the animal a basically complete aspect.

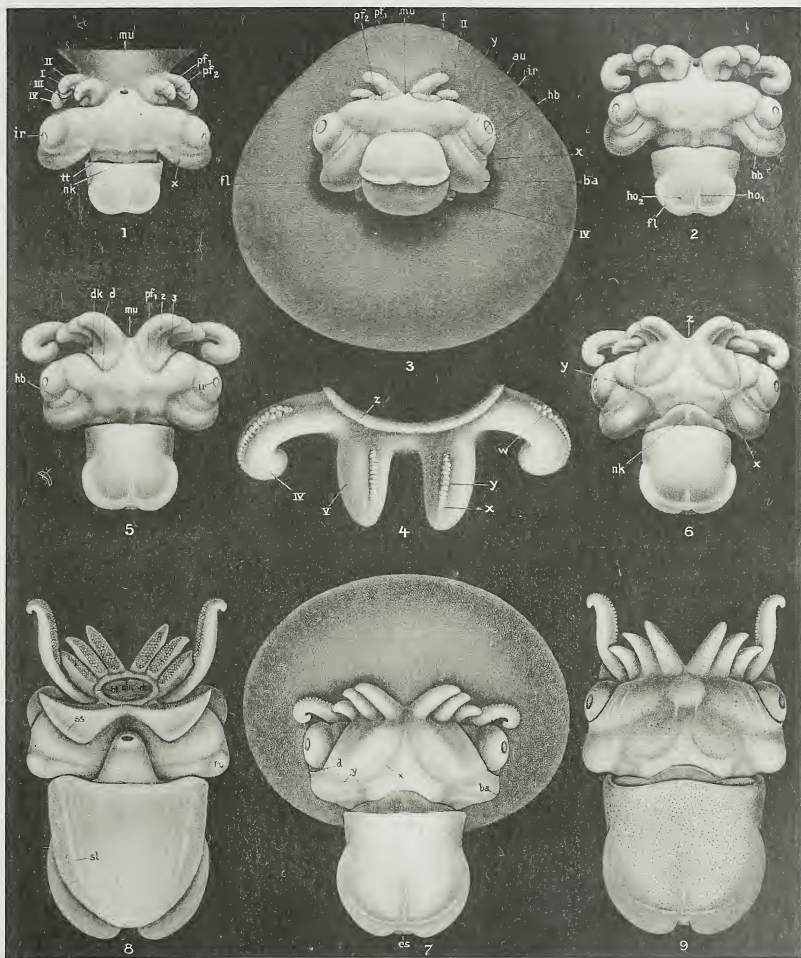


Plate 17: Development of the ventral aspect, and of the mantle cavity of the embryo in *Sepia officinalis*. 16× natural size.

- Fig. 1. Stage IX (Cf. Pl. 3, Fig. 5).
Fig. 2. Stage X (Cf. Pl. 3, Fig. 8).
Fig. 3. Stage XI (Cf. Pl. 4, Fig. 2). x: sucker rudiments.
Fig. 4. Stage XI-XII (Cf. Pl. 4, Figs. 4-6). x: cutting surface.
Fig. 5. Stage XII (Cf. Pl. 4, Fig. 8); y: coelomic pouches containing the branchial hearts.
Fig. 6. Stage XII.
Fig. 7. Stage XIII.
Fig. 8. Stage XIII. The branchial band begins to form; x: posterior limit of head cover.
Fig. 9. Stage XIII-XIV. hb and v still lying far apart!
Fig. 10. Stage XV. hb and v united. x as in Figure 8.
Fig. 11. Stage XV. y: web between ventral and ventrolateral arm begins to form. Kidney papillae are visible, gill lamellae pleated, branchial band *Nautilus*-like.

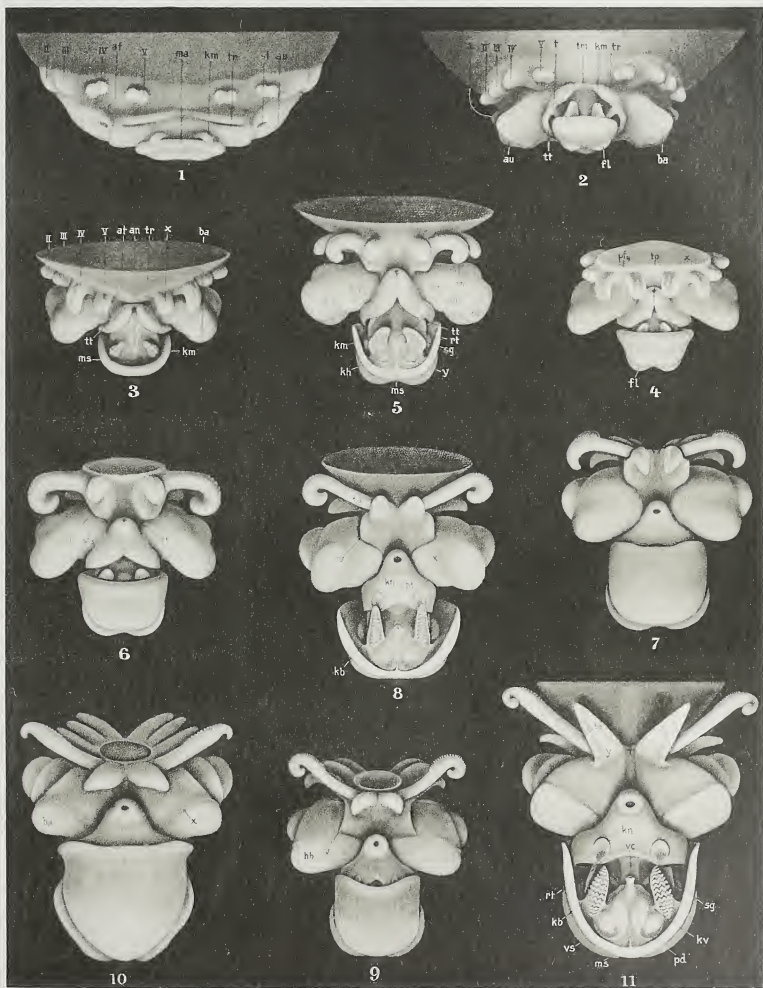


Plate 18: Advanced embryonic stages of *Sepia officinalis*. 16× natural size

- Figs. 1-3. Stage XVII. Fig. 1. Dorsal view with yolk sac in natural position (Cf. Plate 16). x: posterior limit of head cover; y: primary head skin; z: posterior end of extended ventral part of the mantle sac.
- Fig. 2. x=y of Plate 17, Figure 11. Note the distribution of sucker rudiments.
- Fig. 3. Ventral mantle and funnel parts removed. x: coelomic pouch; ax: visceral complex, especially head-foot retractor; ta: entry to tentacle pouch.
- Fig. 4. Stage XVIII. The rotation of the ink sac begins. x: posterior limit of kidney sac. The tentacular stalks grow longer in widening tentacle pouches (ta).
- Fig. 5. Tentacular club at stage XVII-XVIII; suckers still arranged in 8 rows; differentiation of manus and stalk distinct, note the swimming membrane rudiment (at left). 48× natural size.
- Fig. 6. Tentacular club at stage XIX-XX. x: terminal tip; y: swimming membrane; z: protective membrane; 1-8: suckers of original eight longitudinal rows, lying in an oblique transverse row. 48× natural size.



Plate 19: Maturing embryos of *Sepia* (1-6 *S. officinalis*, 7 *S. orbignyana*).

- Figs. 1 and 2. Stage XIX. With small, fragile yolk sac. Viable when prematurely hatched. x: position of posterior edge of cuttlebone. 8× natural size.
- Fig. 3. Mantle cavity at the same stage. Ink sac rotated!
- Figs. 4 and 5. Lateral view of stage XVIII -XIX. 10× natural size. Illustrating the eye lid development. The secondary lid arises as a fold surrounding the primary lid.
- Fig. 6. Opening of the primary lid when contracted, in a similar embryo. The fold of the prospective secondary lid is recognizable by the conspicuous arrangement of the muscular fibres.
- Fig. 7. Embryo of *Sepia orbignyana*. 10× natural size. The pupil (pu) is W-shaped, the primary lid is closed, except at the ocular pore (po), and forms a "cornea". The secondary lid is crescent-shaped, open to the top. In these embryos the fin is strikingly short, a primitive trait (among others).

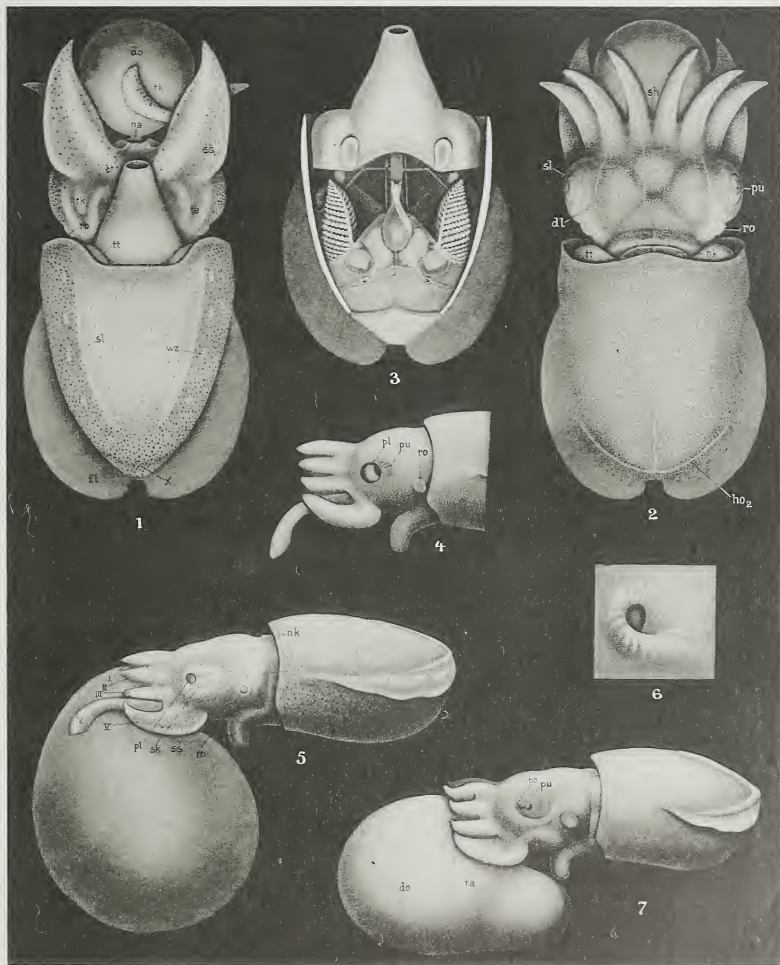


Plate 20: Figures 1-3 *Sepia officinalis*, newly hatched, fully developed.

(In contrast to most hatchlings obtained in the aquarium, these are not prematurely hatched animals!). 8 x natural size. Explanations in Plate 19.

- Fig. 4. Cuttlebone at stage XVIII (Pl. 18, Fig. 4). 16 x natural size. Three siphuncular openings are recognizable, each with a distinct, flat septal neck (finely dotted). The shell plate is uncalcified in the marginal zone (dark), calcified in the remaining parts (light), structurally different in the posterior part (See the text). In the last septum, the anterior ("bulge") part can already be distinguished from the posterior ("fork") part (along the posterior insertion). Of the second septum, the anterior insertion shines through the last septum. The light dots (lines) mark the insertions of the pillars supporting the septa.
- Figs. 5 and 6. Cuttlebone of stage XX (Figs. 1-3). In the dorsal view, the initial chamber is clearly visible, with the excentric addition of subsequent chambers along a curved surface.

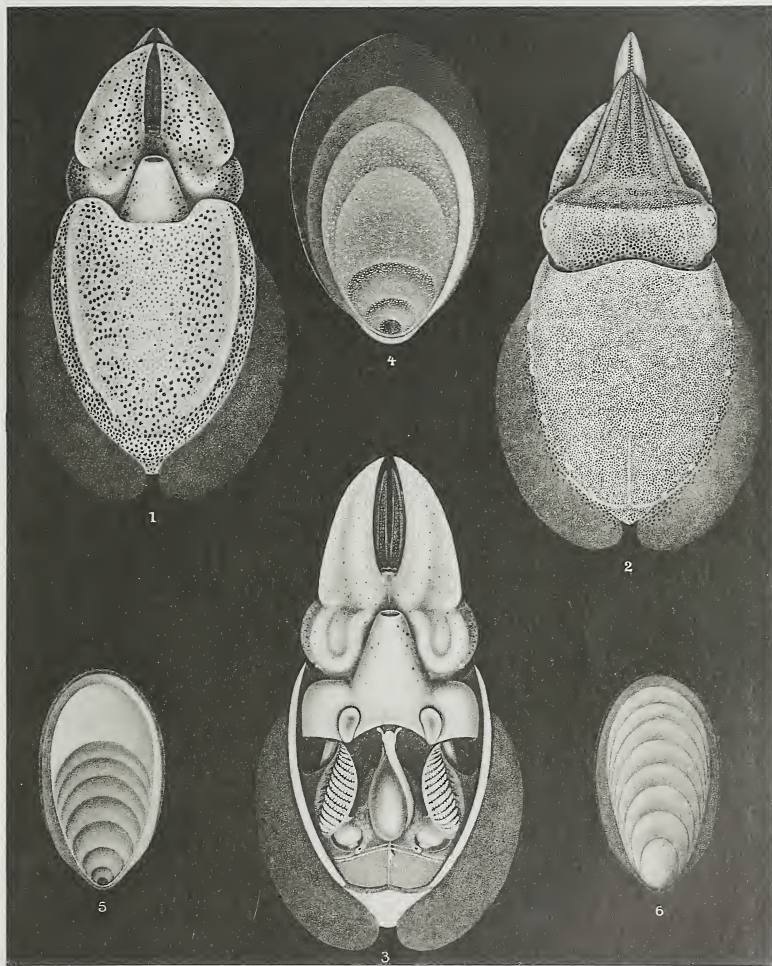


Plate 21: Development of the buccal field and the inner arm surfaces in embryos of *Sepia officinalis*.

- Fig. 1. Buccal field of stage XV. 25× natural size. x: section of yolk envelope.
- Fig. 2. Buccal field of stage XV-XVI. 25× natural size. y: section of removed tentacle; z: section of latero-ventral arm.
- Fig. 3. Buccal field of stage XVI-XVII. 25× natural size. Slightly abnormal. The dorsal buccal lappets (1 and 1a) are not fused (in contrast to Figure 2: bt); thus an interesting case of inhibition appears, similar to the normal condition occurring in the family Enoploteuthidae, which can be considered the protodecapodan primary condition. (Volume 1, page 122).
- Figs. 4-7. Development of a single arm from stage XIII to stage XVI. 48× natural size. In the gutter between the two parts of the arm (y) a ridge is formed that becomes subdivided into narrow papillae (Cf. *Nautilus*). These papillae grow larger and rounder and become arranged in a zigzag pattern; this process is repeated so that the two rows are transformed into four rows. The differentiation at the arm end continues as in a growing plant tip.
- Figs. 8 and 9. Tentacular clubs at stages XV-XVII. 48× natural size. The four rows of suck-ers are changed into eight rows, which is the basis for further differentiations of a *Sepia* club (Plate 18).

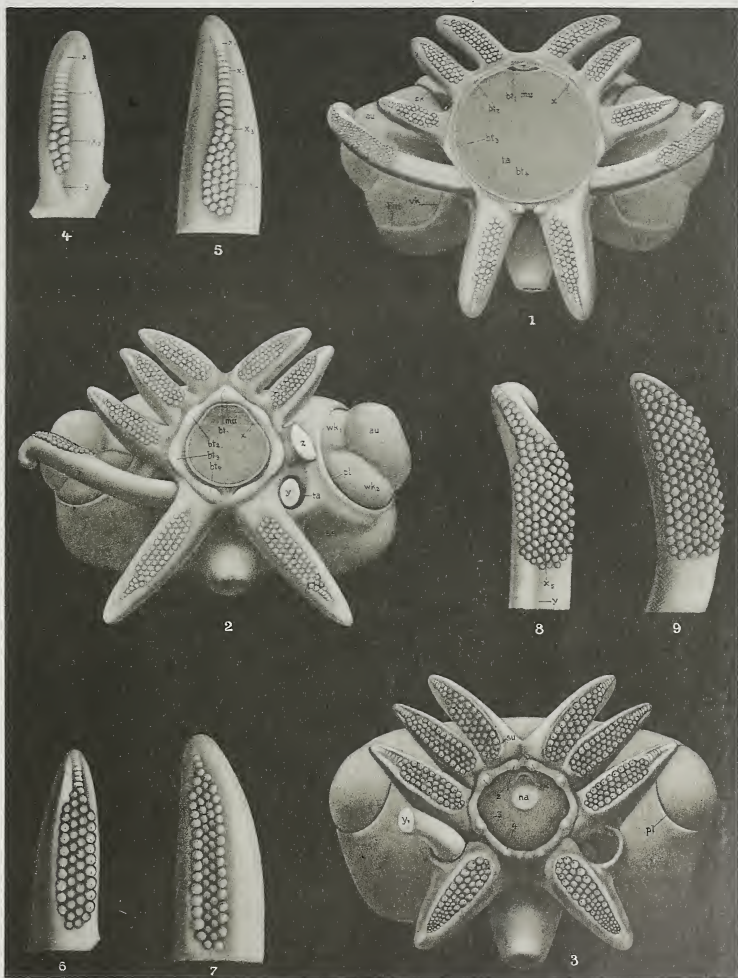


Plate 22: Further development of the buccal field of *Sepia officinalis*.

- Fig. 1. Stage XVIII-XIX. x: infrabuccal part of yolk sac (Cf. Plate 19, Figure 1). 22× natural size.
- Fig. 2. Stage XIX. y: connecting band of a buccal pillar. 20× natural size.
- Fig. 3. Young cuttlefish, postembryonic, 15× natural size. Apart from the retracted tentacles (7, 8), this figure offers the typical picture of a decapod. 1) 4: buccal pillars; I-III: buccal pouches; 5: inner lip; 6: buccal membrane, hiding the outer lip; 7, 8: tentacular clubs; 9: protective membranes uniting at arm base; 10: outer edge of ventral arm; 11: web.
- Fig. 4. The part surrounded by the buccal funnel is opened up. Stage XIX. 22× natural size. One recognizes the widening mouth (Cf. Figure 1), in which the inner lip (il) and the tip of a beak (uk) appear; na: umbilicus.
- Fig. 5. The same. Buccal funnel (schematic) of stage XIX-XX. 20× natural size.
- Fig. 6. The same for stage XX-XIX. 18× natural size. The infrabuccal part of the yolk sac is rapidly reduced by the growing buccal mass.
- Fig. 7. The same for stage XX (typical aspect).

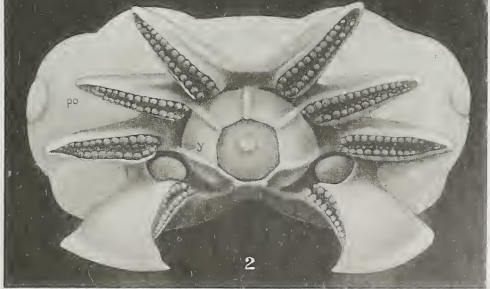
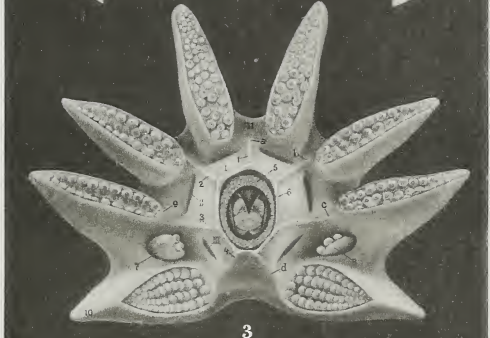
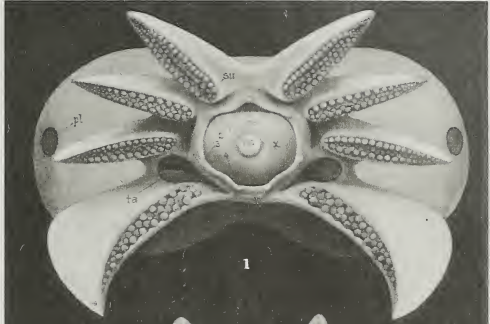
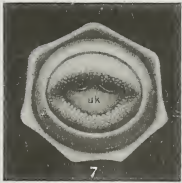


Plate 23: Embryos of Sepiolinae.(Different species of the so-called *Sepiola rondeleti*)

- Fig. 1. *Sepiola ligulata*. Stage VIII-IX. 16× natural size (Cf. Plate 15, Figure 2); y: questionable rudiment (? blood vessel?); x: indication of a proostracal relic in the shell sac; z: nuchal connection, already indistinct in comparison with *Sepia* and *Rossia*!
- Fig. 2. *Sepiola ligulata*. Stage X. 16× natural size (Cf. Plate 15, Figures 3 and 4).
- Fig. 3. *Sepietta oweniana*. Stage XI-XII. 24× natural size.
- Fig. 4. The same embryo, seen from below after removal of the yolk (Cf. Plate 17, Figure 4!).
- Fig. 5. *Sepietta oweniana*. Stage XIII-XIV. 28× natural size (Cf. Plate 16, Figure 6).
- Fig. 6. *Sepiola ligulata*. Stage XIV-XV. 16× natural size. Lid fold complete!
- Fig. 7. *Sepietta oweniana*. Stage XV-XVI. 24× natural size.
- Fig. 8. *Sepietta oweniana*. Stage XVII-XVIII. 22× natural size.
- Fig. 9. *Sepiola ligulata*. Stage XIX. 18× natural size.

Note the transversely extended shape of the ink sac with the bean-shaped (light) luminous glands.

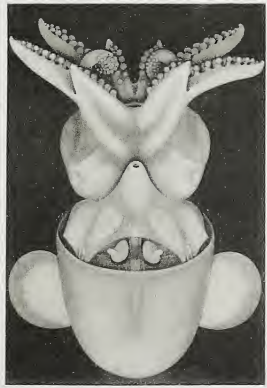
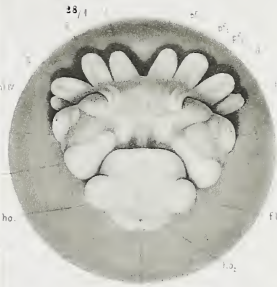
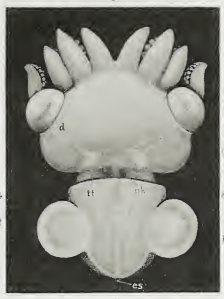
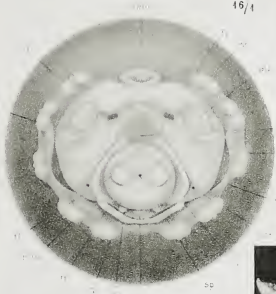
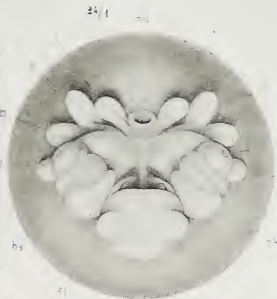
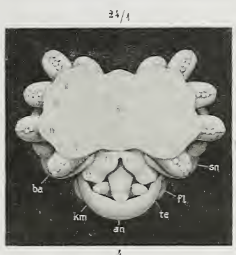


Plate 24: Maturation, cleavage and germinal layer formation in *Octopus vulgaris*.
45× natural size.

Interpretations as in Plate 1! Hitherto undescribed ontogenesis.

- Fig. 1. 2 hours after egg laying. x: first polar body; y: position of the nucleus.
 Fig. 2. (3 hours). Three polar bodies formed.
 Fig. 3. (5 hours). Spreading of formative plasm.
 Fig. 4. (9 hours). First cleavage step.
 Fig. 5. (13 hours). The third cleavage step is prepared (x).
 Fig. 6. (15 hours). 8 cell stage, normal.
 Fig. 7. (15 hours). 8 cell stage, decapod-like (Plate 1, Figure 13).
 Fig. 8. (16 hours). Transition to 16 cell stage.
 Fig. 9. (19 hours). 16 cell stage. The cells x, y can be separated entirely (Fig. 10) as true micromeres, or they can remain in continuity with the yolk (as in x above).
 Fig. 10. (19 hours). Variant of same stage.
 Fig. 11. (22 hours). 23 cell stage; retarded at left.
 Fig. 12. (24 hours). 32 cell stage
 Fig. 13. (24 hours). 32 cell stage; another variant.
 Fig. 14. (28 hours). 66 cell stage
 Fig. 15. (36 hours). 360 cell stage
 Fig. 16. (40 hours). 1200 cell stage; blastoderm complete. Stage. I.
 Fig. 17. (2 days). Endo-mesoderm formation starts. Stage I-II.
 Fig. 18. (2½ days). Endo-mesoderm formation continues. Stage II.
 Fig. 19. (3 days). Endo-mesoderm formation continues. Stage II-III.
 Fig. 20. (3½ days). Endo-mesoderm formation continues. Stage III.

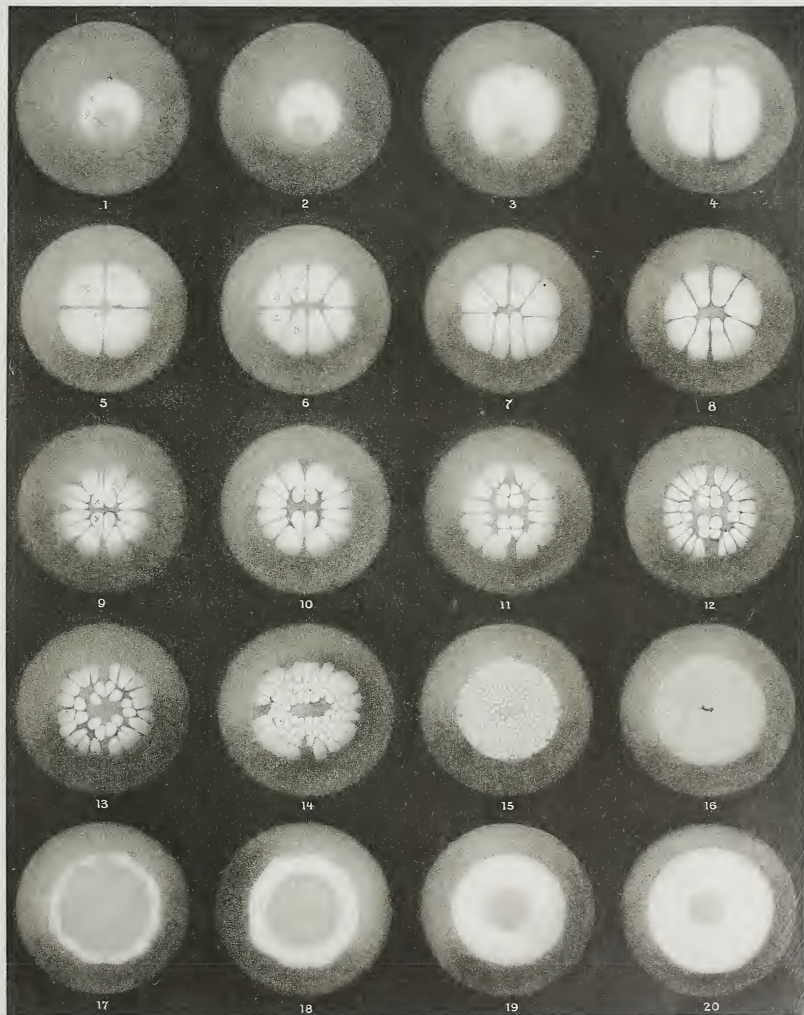
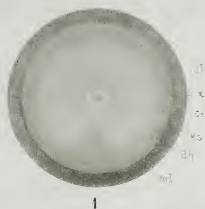


Plate 25: Differentiation of the germinal disc, covering of the yolk, folding processes in *Octopus vulgaris*. 45× natural size.

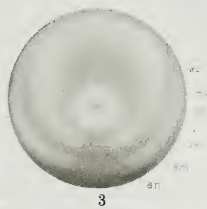
- Fig. 1. Stage IV (4 days), from behind. x: concentration of material for the mantle.
- Fig. 2. Stage V (5 days). Cf. Plates 14 and 2.
- Fig. 3. Stage VI (4 days). x: position of statocyst.
- Fig. 4. Stage VII (7 days). Note the small rudiment of the shell sac and fins.
- Fig. 5. Stage VIII (8 days).
- Fig. 6. Stage IX (9 days).
- Fig. 7. Stage X (10 days).
- Fig. 8. Stage XI (11 days).
- Fig. 9. Stage IV. From the ventral side, illustrating yolk covering.
- Fig. 10. Stage V. From the ventral side, illustrating yolk covering.
- Fig. 11. Stage VI. From the ventral side, illustrating yolk covering.



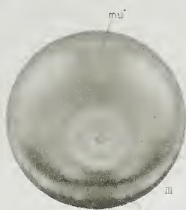
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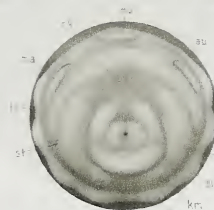
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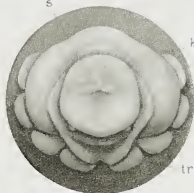
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Plate 26: Stages of folding processes in *Octopus vulgaris*. 45× natural size.

In lateral, ventral and dorsal view.

Fig. 1-3. Stage VII (7 days). x: position of statocyst.

Fig. 4-6. Stage VIII (8 days)

Fig. 7-9. Stage IX (9 days). Cf. Plate 3 and note the late differentiation of the funnel tube rudiment (tr) in connection with the arm crown, independently from the funnel pouches (tt).

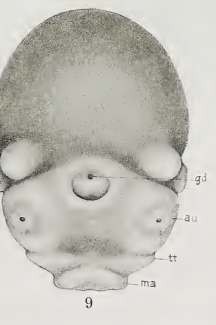
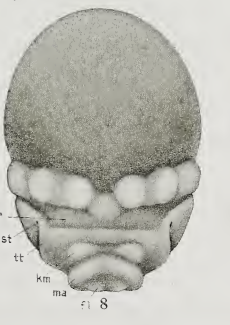
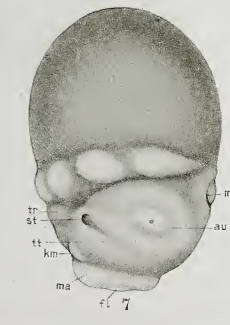
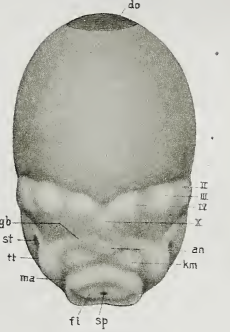
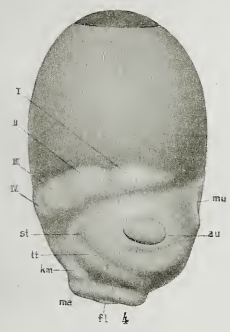
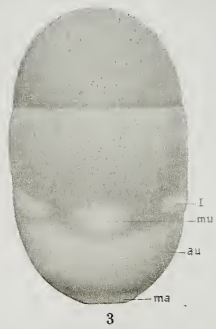
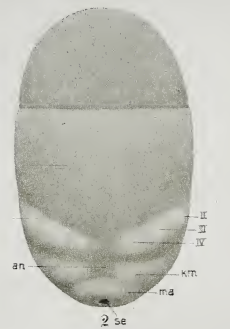
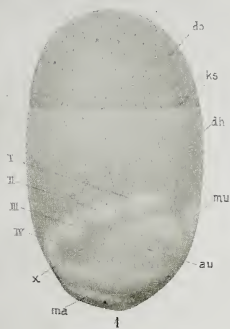


Plate 27: Primary structuring of the embryo in *Octopus vulgaris*.
45× natural size (Cf. Plates 3, 4 and 9).

Figs. 1-3. Stage X (10 days).

Figs. 4-6. Stage XI (11 days).

Figs. 7-9. Stage XII (12 days). y: *Musculus rect. abdominalis* (Cf. Plate 23, Figures 4, 9); z: depression between inner and outer part of arm (Cf. Plate 23, Figure 3). Note the closure of the mouth by a transparent membrane through which it remains visible (Plate 28).

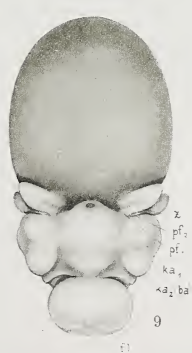
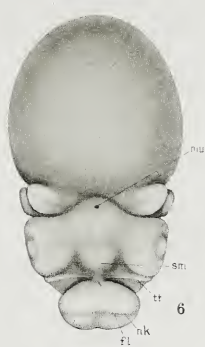
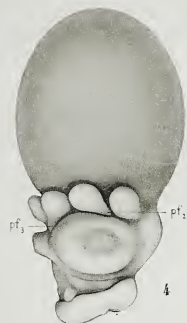
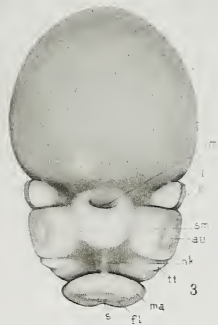


Plate 28: Secondary structuring and rearrangement of the cephalic organs in embryos of *Octopus vulgaris*. 45× natural size.

- Figs. 1-3. Stage XIII (13 days). x: gill lamellae; y: dorsal mantle slit, medially (z) barely visible, penetrating from both sides.
- Figs. 4-6. Stage XIV (15 days). x (in Figure 4): medial limit of head cover; y: posterior limit of head cover.
- Figs. 7-10. Buccal field after removal of the yolk. Figure 7: stage XIII (13 days); z: yolk envelope; y: brachial ganglion at the bottom of the yolk depression; w: passage to inner yolk sac.
- Fig. 8. Stage XV (18 days).
- Fig. 9. Stage XVI (21 days).
- Fig. 10. Stage XIX (28 days). x: remainder of yolk sac; y: terminal flagellum of arm.

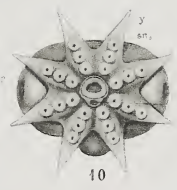
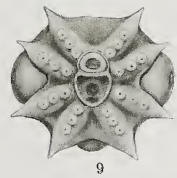
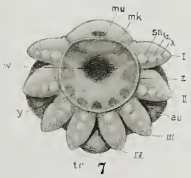
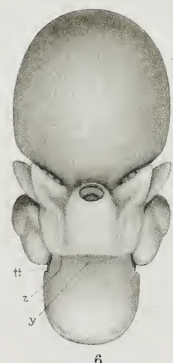
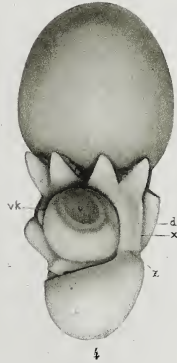
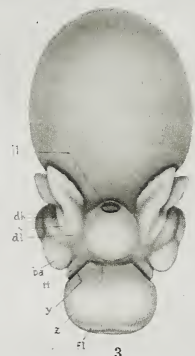
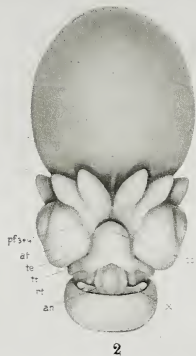
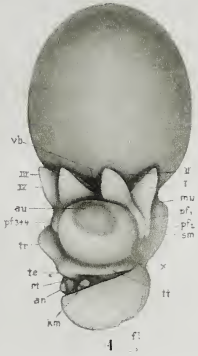
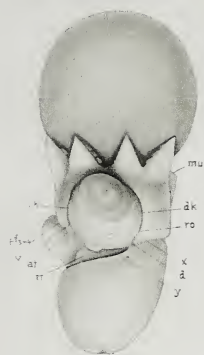
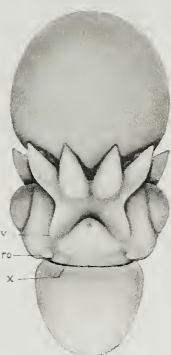


Plate 29: Development of the head covers and lid folds, and of the mantle cavity in embryos of *Octopus vulgaris*. 45× natural size.

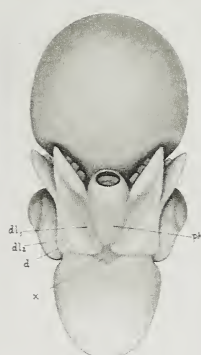
- Figs. 1-3. Stage XV (18 days). Fig. 1, x: seam between head cover and muscular mantle; y: posterior dorsal part of mantle slit with remarkable opening; Fig. 2, x: prospective (preformed) position of the mantle rim on the funnel; Fig. 3, x: remainder of primary integument.
- Fig. 4. Mantle cavity of specimen in Fig. 2. x: mantle section; y: posterior end of visceral sac; z: gill lamellae; w: posterior funnel edge.
- Fig. 5. Mantle cavity of specimen in Fig. 7. x: swollen integument of funnel (muscular tube in light color); m: kidney sac wall.
- Figs. 6-8. Stage XVI (21 days). Fig. 6, x: terminal flagellum of dorsal arm; y: same as x in Fig. 2; Fig. 7: same as before; Fig. 8, x: primary cephalic integument (Cf. pk in Fig. 3).



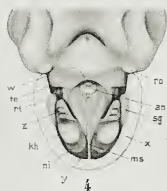
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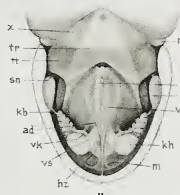
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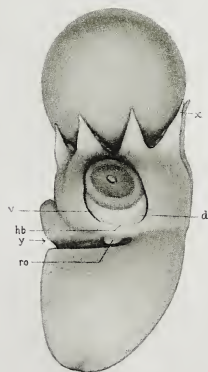
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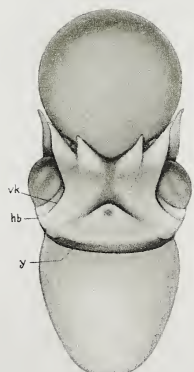
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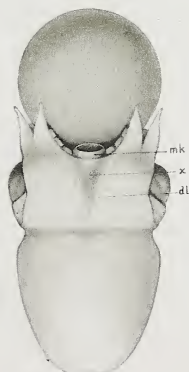
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Plate 30: Maturing embryos of *Octopus vulgaris*. 45× natural size.

- Figs. 1-3. Stage XVIII (24 days old). x: as in Fig. 2 of Plate 29; y: same as x in Fig. 1 of Plate 29.
- Figs. 4-6. Stage XIX-XX (28 days old). Note the spines breaking out from the small glandular sacs visible at the previous stage; they subsequently split up to form minute brushes (vol. 1, Pl. 9, Fig. 1).

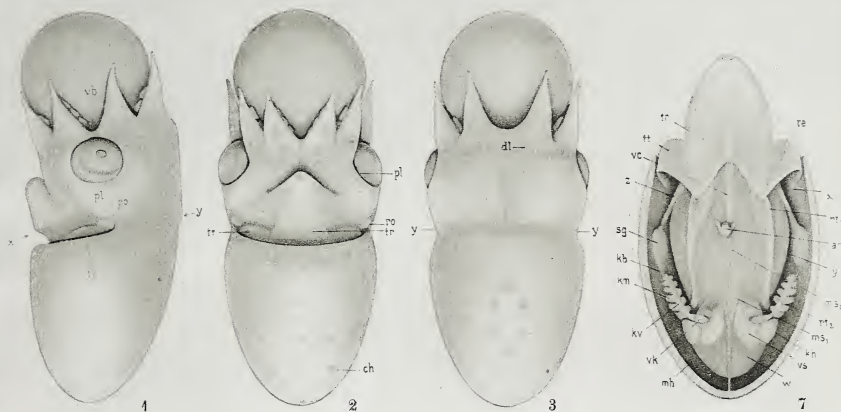


Plate 31: Embryos of *Tremoctopus violaceus*. 45× natural size.

From an egg mass conserved in the Zoological Collections of Munich; at first sight (1914) I tentatively identified it as an *Argonauta* egg mass, given the great similarity of the embryos with those of this genus. The material is probably due to A. Kölliker; it exactly corresponds to his description.

Figs. 1 and 2. Stage XI-XII. x: dorsal mantle furrow.

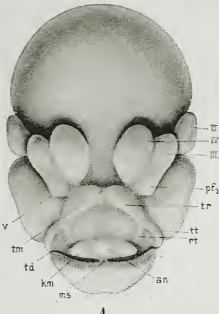
Figs. 3 and 4. Stage XVI. x: dorsal mantle furrow.

Fig. 5. Stage XX. Newly hatched.

Fig. 6. Stage XIX (Cf. Volume 1, Plate 10, Figure 4). y: depression for the funnel corners (mantle attachment); x: posterior end.

Fig. 7. Buccal field (of stage XVI), like Plate 28, Figure 9. y: yolk; z: yolk envelope.

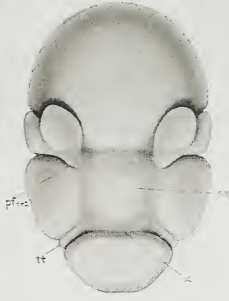
Fig. 8. Buccal field of stage XIX, more strongly enlarged. x_1 , x_2 : new sucker rudiments formed during embryonic development (Cf. Plate 28, Figure 10).



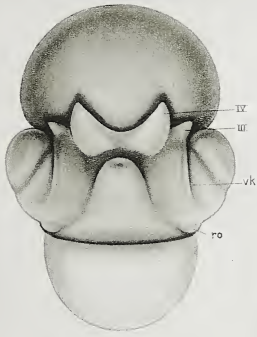
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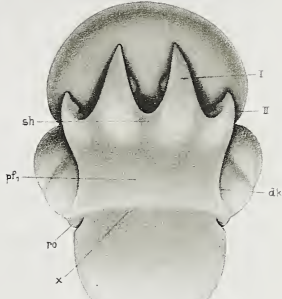
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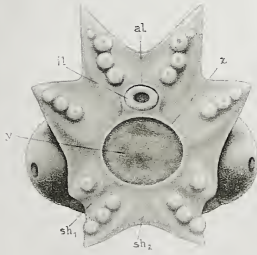
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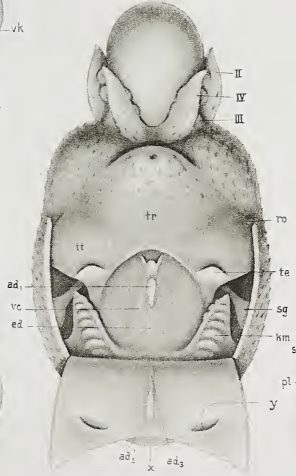
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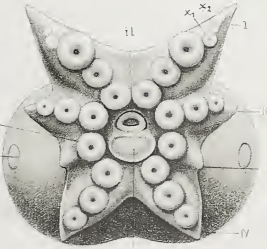
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Plate 32: Early embryos of *Argonauta argo*. 70× natural size.

The ontogenesis of this form, which is particularly interesting, is shown here in greater detail (starting from egg laying) than was done for the preceding ones. Cleavage is achieved inside the oviduct, according to the same pattern as in *Octopus vulgaris* (Plate 24); even more advanced stages can be retained in the oviduct.

Figs. 1-4. Stages I-IV, from behind. x: gaps in the blastoderm.

Figs. 5-7. Covering of the yolk. Stages I, IV, V-VI.

Figs. 8-10. Buccal field (of stage XVI).

Figs. 11-13. Stage VIII. x: furrow between arm crown and head anlage; y: furrow between head anlage and funnel pouches.

Figs. 14-16. Stage IX.

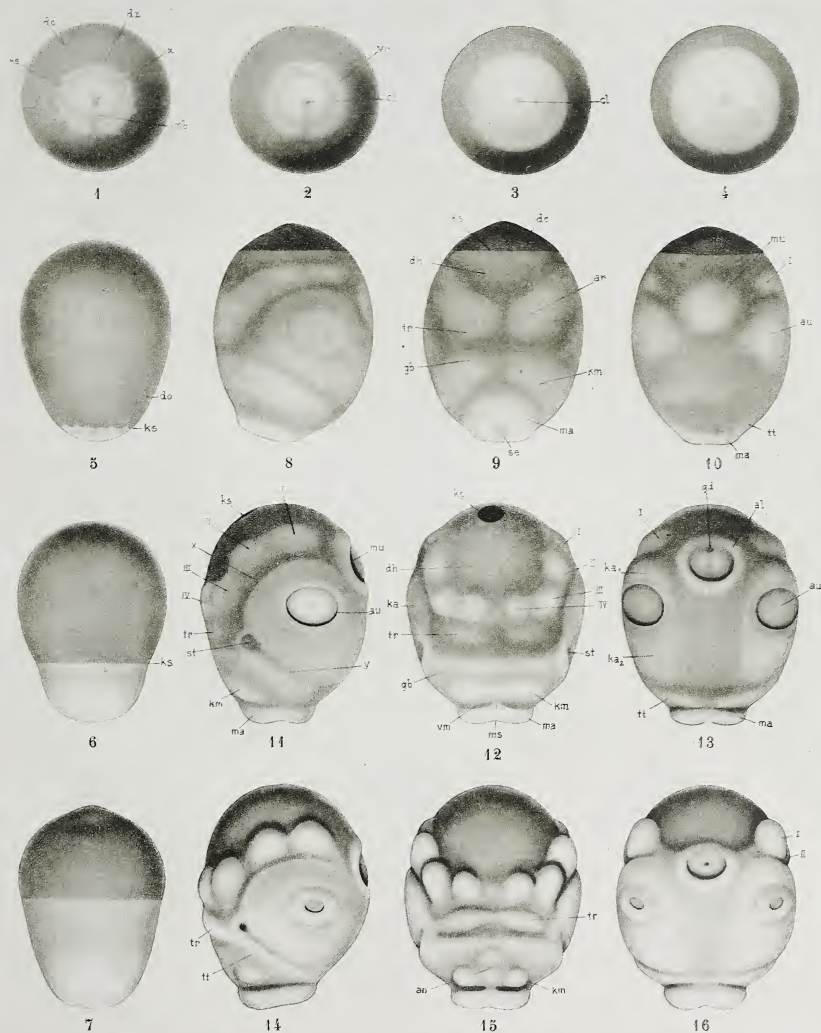


Plate 33: Embryos of *Argonauta argo*. 70× natural size.

- Figs. 1-3. Stage X. x: dorsal mantle furrow, in octopods never getting deeper in the medial point (Cf. Plate 27).
- Figs. 6-8. Stage XI. x: closure of shell sac.
- Figs. 4 and 5, 9 and 10. Mantle rudiments from behind, stages VII, VIII, IX, X. x: gap of muscular mantle, closing progressively (Cf. Fig. 9 with Fig. 7 of Plate 15).
- Figs. 11-13. Stage XII. x: same as in Fig. 1; y: same as z in Fig. 9 of Plate 27. Note the beginning shift of the arm pillars.

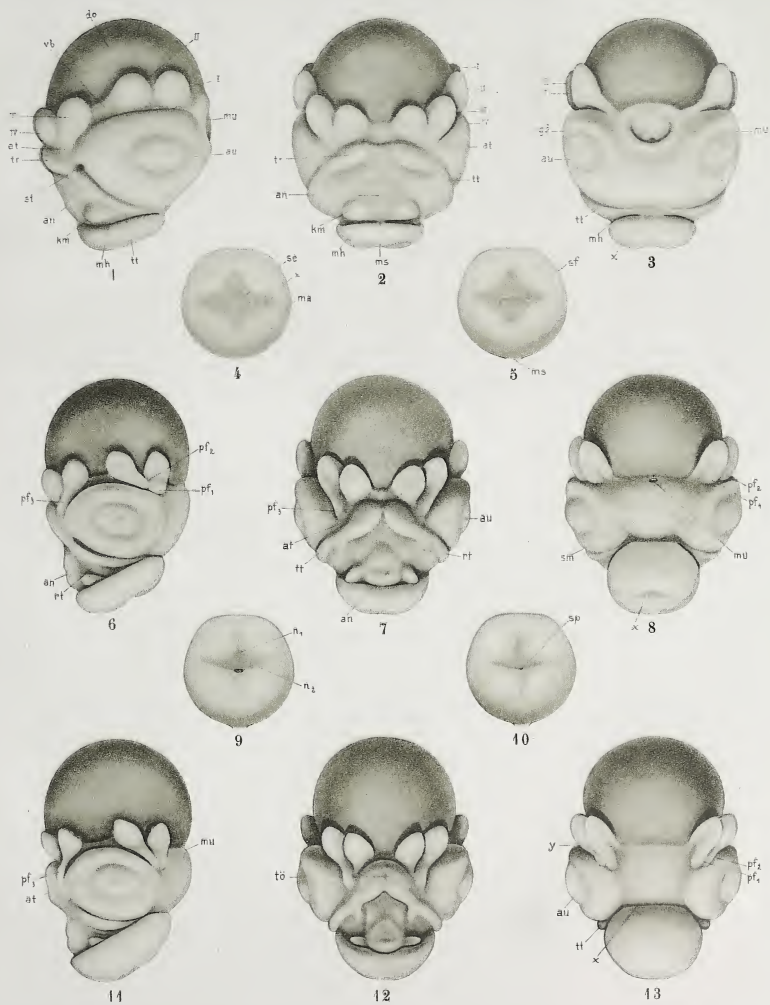


Plate 34: Embryos of *Argonauta argo*. 70× natural size.

- Figs. 1-3. Stage XIII. Fig. 1, x: dorsal, y: lateral mantle furrow. Fig. 2, x same as Plate 29, Figure 2; y: same as Plate 27, Fig. 8. Fig. 3, x: position of invaginated mouth; y, z: parts of the cephalic anlage (white body); w: dorsal mantle slit.
- Figs. 4-6. Stage XIV. x: posterior limit of head covers.
- Figs. 7-9. Stage XV. x: growing arm tip, corresponding to the prospective "shell-forming" arm in the female. The formation of the head covers from the arm pillars is particularly evident here, as is the formation of the primary lid.

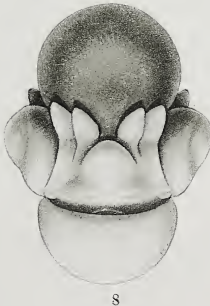
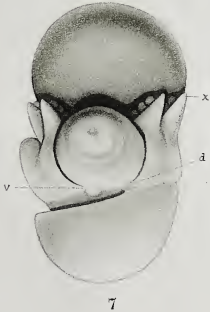
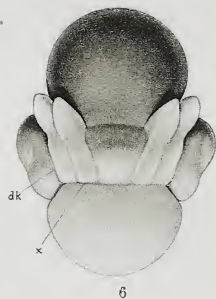
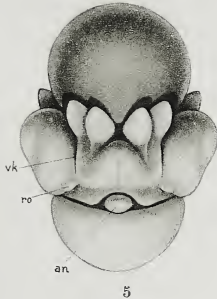
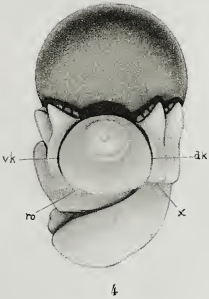
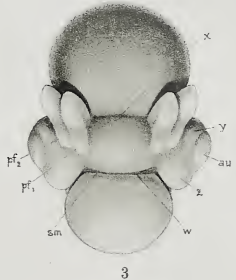
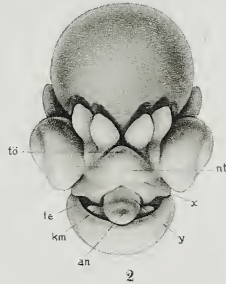
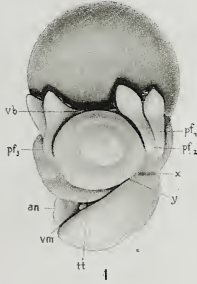


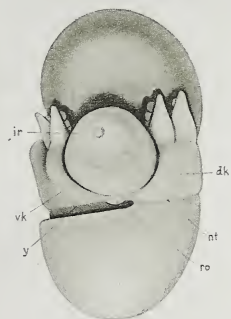
Plate 35: Embryos of *Argonauta argo*. 70× natural size.

Figs. 1-3. Stage XVI. Fig. 1, y: same as x in Plate 29, Fig. 2. Fig. 3, y: dorsal mantle furrow.

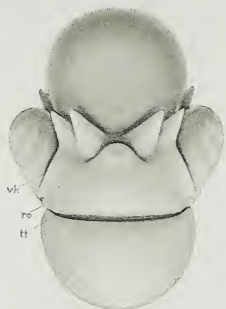
Figs. 4-6. Stage XVII.

Figs. 7-9. Stage XVIII. x: same as in Plate 34, Fig. 7.

The definitive octopodan body is complete in its general outline; the covering of the head is finished.



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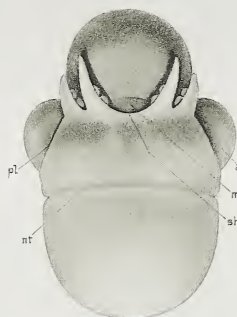
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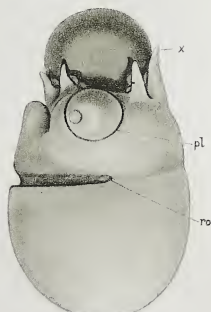
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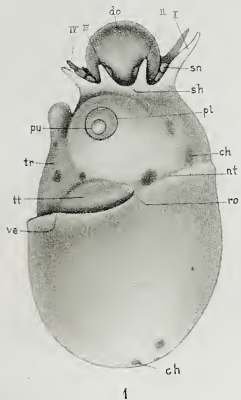


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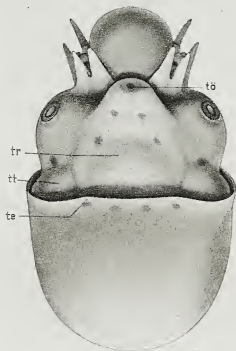
Plate 36: Embryos and hatchlings of *Argonauta argo*. 70× natural size.

Figs. 1-3. Stage XIX.

Figs. 4-6. Stage XX. Fig. 4, x: protracted, bulging web; y: integumental spine. Fig. 5, x: same as above; y: mantle attachment (knob, cf. Plate 31, Fig. 6); z: funnel attachment; w: posterior edge of funnel tube. Fig. 6, x: lateral mantle rim.



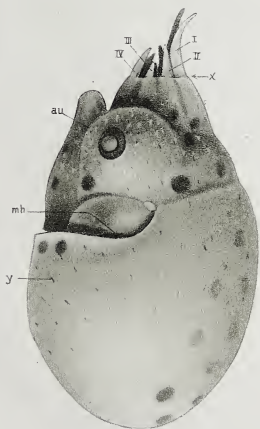
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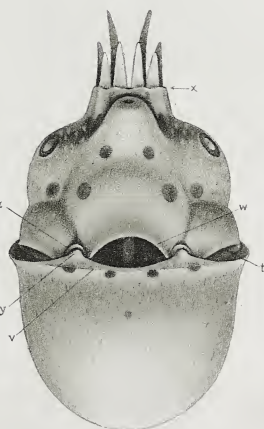
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Plate 37: Embryos of *Argonauta argo*. 70× natural size

(Figures 1-3) and *Ocythoë tuberculata* 40× natural size

(Figures 4-9, from eggs sampled in the oviduct).

Fig. 1. *Argonauta*. Stage XX. From the buccal side, with spread arms. x: mantle rim insertion on the head.

Fig. 2. *Argonauta*. Stage XIX. Ventral mantle cavity opened up.

Fig. 3. *Argonauta*. Stage XIX. Dorsal mantle cavity opened up. z: mantle section; y: mantle nerve; x: dorsal side of visceral complex.

Figs. 4 and 5. *Ocythoë*. Stage IX. Fig. 5, y: same as in Plate 23, Fig. 3; x: ocular pore.

Figs. 6 and 7. *Ocythoë*. Stage XII-XIII. x: part of cephalic anlage (white body).

Figs. 8 and 9. *Ocythoë*. Mantle rudiments of stages IX and XI. x: limit of the centripetally advancing muscular mantle tissue. Note the progressively indistinct fin rudiments (fl) in *Argonauta* (Plate 33), and the relatively large yolk mass (compare Pl. 37, Fig. 4 and Pl. 33, Fig. 2); the yolk sac of *Argonauta* appears reduced, similar to the yolk sac of oegopsids among the decapods (Plates 8 and 9).

